A CONTRIBUTION TO THE EMBRYOLOGY OF SOME SOLANACEAE

ABSTRACT

THESIS SUBMITTED FOR THE AWARD OF THE DEGREE OF

Doctor of Philosophy

IN

BOTANY

By

Shama Parveen Siddiqui

DEPARTMENT OF BOTANY
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The present investigation deals with the embryology of Solanum hispidum Pers., S. furcatum Dun., S. retroflexum Dun., S. douglasii Dun. and S. cornutum Lam.

The habit, external morphology and inflorescence of the above mentioned species have been described.

The flowers are pentamerous and actinomorphic in S. hispidum, S. furcatum, S. retroflexum and S. douglasii while in S. cornutum the flowers are zygomorphic. Occasionally the flowers may be tetramerous in S. hispidum. The calyx lobes are gamosepalous, bell-shaped and persistent in all the species described here. The calyx is accrescent in S. cornutum. The corolla is gamopetalous and campanulate in S. hispidum, S. furcatum, S. retroflexum and S. douglasii. However in S. cornutum the corolla is zygomorphic. The stamens are epipetalous. The anthers are bithecous and 4-chambered. The ovary is bicarpellary, syncarpous and bilocular with swollen axile placenta. The stigma is capitate in S. furcatum, S. retroflexum and S. douglasii while in S. hispidum and S. cornutum its is lobed. Heterostyly has been observed in S. hispidum. The fruit is berry.

The floral organogeny takes place in acropetal succession.

The anthers are quadrangular in transection. The development of anther wall layers in all the five species conforms to the Dicotyledonous type. In a mature anther

three layers of cells intervene the epidermis and sporogenous layer. The endothecium is single layered in S. furcatum and S. douglasii, 2-layered in S. retroflexum, 4-layered in S. hispidum and 2-4-layered in S. cornutum. The endothecium is devoid of fibrous thickenings except in the tip region. Next to the endothecium is middle layer which is single layered in S. retroflexum, 2-layered in S. hispidum and S. furcatum, 3-layered in S. douglasii and 2-4-layered in S. cornutum. These layers are sandwitched between the endothecium and the tapetum. The tapetum is generally binucleate in all the species, sometimes 2-4 nucleate in S. furcatum and S. cornutum. The tapetum and middle layers degenerate during the development of pollen grains.

The dehiscence of the anther is porous in S. furcatum, S. retroflexum and S. douglasii and porous as well as by longitudinal slit in S. hispidum. In S. cornutum the dehiscence is porous as well as with the help of pores formed at different intervals in the longitudinal suture.

The microspore mother cells undergo meiosis. The divisions in all the microspore mother cells of an anther may not be synchronous. Thus different divisional stages of microsporogenesis have been observed in all the four chambers of the same anther.

The microspore tetrads are tetrahedral, occasionally they may be isobilateral in S. hispidum, S. douglasii and S. cornutum and decussate in S. furcatum and S. retrofle-

xum. Rarely rhomboidal and decussate arrangements have been observed in S. hispidum, S. douglasii and S. cornutum. Isobilateral and rhomboidal microspore tetrads may rarely occur in S. furcatum and S. retroflexum.

Generally the pollen grains are tricolporate in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum. Tetracolporate pollen grains may alsooccur in S. furcatum, S. retroflexum and S. cornutum. Multicolporate pollen grains have been observed in S. retroflexum.

Variations in the number and size of the nuclei in the pollen grains have also been observed. The pollen grains are shed at 2-nucleate stage in S. hispidum, S. furcatum and S. cornutum, while in S. retroflexum and S. douglasii they are shed at 3-nucleate stage.

Polysiphonous condition and in situ germination of pollen grains have been observed in S. cornutum.Pollen sterility is more common in S. hispidum.

The ovules are anatropous, unitegmic and tenuinucellate. The innermost layer of the integumentdifferentiates as endothelium in all the five species.Hypostase has been observed in the species described heralt persists upto the mature embryo sac stage and degenerates after fertilization.

The female archesporium is hypodermal in origin.It is usually 1-celled in S. hispidum,S. furcatum, S.retroflexum, S. douglasii and S. cornutum. Occasionally it may be 2-celled in S. hispidum, S. furcatum,S. retro-

flexum and S. cornutum, 3-celled in S. douglasii and S. cornutum and upto 5-celled in S. hispidum. Accessory archesporial cells have been observed in S.hispidum and S. douglasii. The archesporial cell directly functions as megaspore mother cell. The megaspore mother cells undergo meiosis and produce megaspore tetrads.The megaspore tetrads are generally linear in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum. Sometimes the megaspore tetrads may be T-shaped in S. furcatum. Inverted T-shaped megaspore tetrads may rarely develop in S. hispidum and S. cornutum. In an exceptional case in S. retroflexum an isobilateral megaspore tetrad has been observed. In another case the megaspore tetrad may be almost rhomboidal in S. cornutum. Polyspory has been observed in S. hispidum.

Usually the chalazal megaspore is functioning and the remaining three degenerate. Considerable variations in the number and position of healthy megaspores in a tetrad have been observed in S. hispidum,S. furcatum,S. retroflexum, S. douglasii and S. cornutum.

The development of female gametophyte is of monosporic 8-nucleate Polygonum type in the species described here. The polar nuclei fuse before the entry of pollen tube into the embryo sac in S. furcatum, S. retroflexum and S. douglasii while in S. hispidum and S. cornutum they fuse at the time of fertilization. The antipodal cells are ephemeral. Variations in the number of embryo sac nuclei and their organization have also been obser-

ved in S. furcatum, S. retroflexum and S. cornutum. Twin sacs have been observed in S. retroflexum.

Pollination is anemophilous. The pollen grains germinate on the stigma. The pollen tubes creep between the stigmatic papillae and enter the stylar tissue. They grow down through the intercellular spaces of the stylar tissue, reach the ovarian cavity and finally enter the ovules through the micropyle.

One synergid is usually des-troyed during the entry of the pollen tube into the embryo sac. Later the other synergid also is destroyed during the act of fertilization. One male gamete fuses with the egg and the other with the secondary nucleus in S.furcatum, S. retroflexum and S. douglasii, while in S. hispidum and S.cornutum the second male gamete fuses with the polar nuclei simultaneously.

The development of endosperm is ab initio Cellular in S. hispidum, S. furcatum, S. retroflexum,S. douglasii and S. cornutum. The first division in the primary endosperm cell is transverse forming a primary micropylar and primary chalazal endosperm chambers. The division in both the primary endosperm chambers is longitudinal.The development of endosperm in S. hispidum could not be followed successfully after 4-celled stage because of abnormal behaviour of endothelium, whose cells proliferate and produce adventive embryos.

The second division in the primary micropylar and

primary chalazal endosperm chamber is longitudinal producing 8-celled endosperm in S. furcatum. In S.retroflexum the second division in the primary micropylar endosperm chamber is transverse while in chalazal endosperm chamber the division is longitudinal. In S.douglsii the second division in the cells of primary micropylar and primary chalazal endosperm chambers is transverse. The divisions become irregular after the 4-celled endosperm in S. cornutum.

Considerable variations in the plane and sequence of early cell divisions in the development of endosperm have been observed in S. furcatum, S. retroflexum, S. douglasii and S. cornutum.

The proembryonic tetrads are linear and the embryogeny conforms to the Myosotis variation of Chenopodiad type in S. hispidum and S. cornutum. The embryogeny in S. furcatum, S. retroflexum and S. douglasii conforms to the Nicotiana Variation of Solanad type. However, Myosotis variation of Chenopodiad type of embryogeny may sometimes occur in S. retroflexum.

The proembryonic tetrad may sometimes be T-shaped in S. furcatum and rarely in S. retroflexum and S. cornutum and the embryogeny conforms to Ruta variation of Onagrad type.

Variations in the number and position of cotyledons in the mature embryos have been observed in S. hispidum. Polyembryony has been observed in S. hispidum. In addi-

tion to the zygotic embryo a number of adventive embryos may arise from the endothelium. In one exceptional case twin sacs developed in the same ovule. In one sac normal zygotic linear proembryonic tetrad developed while in the other the cavity of the embryo sac is completely filled with endothelial embryos.

Rarely the antipodal cells may divide, redivide and form an undifferentiated embryonal mass of cells at the chalazal end of the embryo sac in S. cornutum.

The ontogeny and structure of seeds have been described. The mature seeds are kidney-shaped. Anatomically the seed comprises a seed coat, persistent endosperm and a mature curved dicotyledonous embryo.

The seed coat comprises an epidermis in S. furcatum and S. cornutum, while in S. retroflexum the seed coat consists of an epidermis and 5-8 layers of integument. In S. hispidum the seed coat consists of an epidermis and 3-4-layered thick walled endothelium, while in S. douglasii the persistent endothelium is single layered with fibrous thickenings. The endothelium degenerates during seed development in S. furcatum, S. retroflexum and S. cornutum.

The epidermis of seed coat is main mechanical layer. It is single layered in S. hispidum, S. furcatum and S. cornutum and at places it becomes 1-2 layered in S. retroflexum and S. douglasii. The cells of the epidermis develop sclerotic thickenings in the inner portion while

the outer region develops only rod-like fibrous thickenings.

The cells of the persistent endosperm possess starch grains and reserve food material in all the species described here. The endosperm in S. furcatum, S. retroflexum, S. douglasii and S. cornutum occupies a large portion of interior space of the seed and extends between the coiled embryo and this part of endosperm is characterized by a bulbous coma head and a slender coma stem.

The affinities of the Solanaceae with the allied families on the basis of embryological features have been discussed. Also the evolutionary trends in the genus Solanum itself have been brought out.

Dedicated to My Father
Alhaj Dr. Rashid A. Siddiqui

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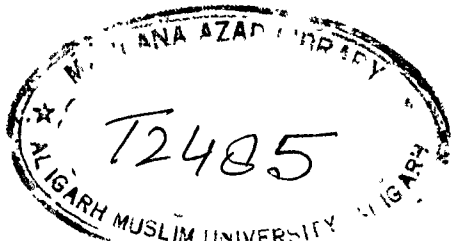

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"He it is WHO sendth down water from the sky, and therewith we bring forth vegetation of every kind; We bring forth the green buds from which are derived thick-clustered grains, ... observe upon the fruit thereof when they (plants) bear fruits, and upon its ripening. Lo! here in verily are portents for people who believe".

AL-QUR'AN

(Al-An'am:12:100)

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CERTIFICATE

This is to certify that the work presented in this thesis entitled "A contribution to the embryology of some Solanaceae" is the original piece of research work carried out by Mrs. Shama Parveen Siddiqui under my supervision and guidance and has not been submitted elsewhere for the award of any other degree or diploma.

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Shama

(SHAMA P. SIDDIQUI)

PREFACE

The main thesis deals with the embryology of *Solanum hispidum* Pers., *S. furcatum* Dun., *S.retroflexum* Dun., *S. douglasii* Dun. and *S. cornutum* Lam.

Following research papers have also been published

1. Effect of gamma irradiation on seed germination, seedling growth and cotyledonary stomata of *Abelmoschus esculentus* Moench.
   Proc. Symp. Environ. Biol. 249-252, 1979 (with Saeed A. Siddiqui, R. Ahmad, F.A. Khan and S. Ahmad).
2. The development of gametophytes in *Hymenodictyon excelsum* Wall.
   Sci. & Environ. 1: 61-64, 1979 (with S.A. Siddiqui).
3. Structure and ontogeny of stomata and trichomes on the leaves of some *Solanum* species.
   Geophytology 10: 189-192, 1980 (with S.A. Siddiqui and R. Ahmad).
4. The development of endosperm and embryo in *Hymenodictyon excelsum* Wall.
   Sci. & Environ. 2: 181-183, 1980 (with S.A. Siddiqui and R. Ahmad).
5. The development of endosperm, embryo and seed in *Solanum khasianum* Clarke.
   Geophytology 11: 154-157, 1981 (with F.A. Khan and S.A. Siddiqui).

6. The development of gametophytes in Hamelia sphaerocarpa Jacq.
   Jour. Sci. Res. 4: 47-49, 1982 (with S. A. Siddiqui and F.A. Khan).
7. The development of gametophytes in Ixora bundhuca.
   Plant Sci. Accepted (with S.A. Siddiqui).
8. The development of endosperm, embryo and seed in Solanum douglasii Dun.
   Flora Accepted (with S.A. Siddiqui)
9. The development of gametophytes in Solanum furcatum Dun.
   Communicated (with S.A. Siddiqui).
10. The development of endosperm, embryo and seed in Solanum hispidum Pers.
    Communicated (with S.A. Siddiqui).

CONTENTS

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INTRODUCTION

Solanaceae are a fairly natural assemblage of plants. Majority of the systematic botanists agree to its position in Sympetalae.However, there is difference of opinion regarding its exact taxonomic relationships. Bentham and Hooker (1873-1876),Bessey (1893), Cundersen (1950), Benson (1957) and Cronquist (1968) placed the family in the order Polemoniales. Solanaceae is placed in between Convolvulaceae and Polemoniaceae in Bentham and Hooker's classification. In Bessey's (1893) treatment Polemoniaceae and Convolvulaceae preceded Solanaceae. Gundersen (1950) is of the opinion that Solanaceae is better placed between Nolanaceae and Scrophulariaceae, while the Polemoniales of Benson (1957) include Convolvulaceae, Hydrophyllaceae, Solanaceae, Polemoniaceae, Boraginaceae and Nolanaceae. However, Benson (1957) regards that the Solanaceae have closest relationship with the Scrophulariaceae. According to Takhtajan (1966) also Solanaceae is closely related to Scrophulariaceae. Families Nolanaceae, Solanaceae, Convolvulaceae, Cuscutaceae, Menyanthaceae, Polemoniaceae, Hydrophyllaceae and Lennoaceae constitute the order Polemoniales of Cronquist (1968).

Engler and Prantl (1895), Wettstein (1935), Rendle (1952) and Melchior (1964) placed the family in the order Tubiflorae alongwith Nolanaceae,Convolvulaceae and Scrophulariaceae. Porter (1959) kept it in the

order Scrophulariales together with Bignoniaceae, Orobanchaceae, Lentibulariaceae and Scrophulariaceae. Hutchinson (1959, 1964) on the other hand is of the opinion that Solanaceae, Convolvulaceae and Nolanaceae form a natural assemblage and calls the order Solanales.

The family Solanaceae is one of the largest Bicarpellatae families having 90 genera and about 2000 species (Willis, 1966). A large number of plants of the family have great economic importance and are known for medicinal, food and ornamental values. The genus Solanum is one the largest in the plant kingdom being represented by about 2000 species (See Gbile, 1976).

Inspite of the morphological and embryological peculiarities of the investigated Solanums only about half a score of its species have been investigated embryologically (Nanetti, 1912; Young, 1922, 1923; Bhaduri, 1932, 1935; Dnyansagar and Cooper, 1960; Saxena and Singh, 1969a,b; Mohan, 1970; Ahmad and Siddiqui, 1981; Khan and Siddiqui, 1981). A perusal of earlier literature on the embryology of Solanums shows the paucity of adequate data on the comparative morphology and embryology as well as the sequential development of seed in majority of the described species.

Considering the number of species and the work done on the embryology of Solanums it was considered

desirable to investigate some more species of the genus and see if embryological features could be helpful in tracing the evolutionary trends within the genus itself and the relationships with the allied families.

MATERIALS AND METHODS

The identified seeds of Solanum cornutum Lam. were acquired by Dr Saeed A. Siddiqui from Professor F. Markgraph, Botanische Garten und Institut fur Systematische Botanik der Universitat Zurich, Germany and were very kindly handed over to me. The seeds were sown in pots and plants were raised.

The flower buds and fruits of different developmental stages of Solanum hispidum Pers., S. furcatum Dun., S. retroflexum Dun., S. douglasii Dun. and S. cornutum Lam. were collected from the garden of the department and fixed in formalin-acetic-alcohol. The materials were dehydrated in alcohol xylol series and embedded in paraffin wax. Sections were cut at 8-12 μ and mounted on the slides. The preparations were stained with safranin and fast green combination.

Young flower buds were also fixed in Carnoy's fluid for 40 minutes and then transferred to Propionic acid saturated with ferric acetate. After 24 hours the buds were transferred to 70% alcohol. Anther squashes were made for microsporogenesis in 0.5% propionocarmine. Slides were made permanent in NBA series and mounted in Canada balsam.

REVIEW OF LITERATURE

The earlier contribution on the embryology of Solanaceae have been reviewed by Schurhoff (1926), Schnarf (1931), Bhaduri (1935, 1936), Davis (1966) and Varghese (1967). Johansen (1950) has summarized the literature on the embryogeny of the family. Besides, the monographs on Nicotiana (Goodspeed, 1954) and Datura (Avery et al., 1959) contain good deal of information on the embryology of these two genera. The detailed review on the embryology of Solanaceae is described in the following pages.

MICROSPORANGIUM, MICROSPOROGENESIS AND MALE GAMETOPHYTE

The microsporangium in Solanaceae is tetrasporangiate. The anther wall development conforms to the Dicotyledonous typeof Davis (1966), except in Withania somnifera (Ram and Kamini, 1964) where it follows the Basic type of Davis (1966). According to Singh and Saxena (1968) the development of anther wall layers in Solanaceous members studied by them conforms to the Dicotyledonous and Basic types. However, Jos and Singh (1968) have described Monocotyledonous type of anther wall development in Nicotiana. The epidermal cells of a mature anther are tangentially elongated. In Lycium europaeum (Jain, 1956) the protoplast of the epidermal cells shrinks at the shedding time of the pollen grains and their outer tangential walls develop cuticular dentation. Copious amount of starch is deposited in the cells of epidermis in Withania somnifera (Ram and

Kamini, 1964). The epidermis is persistent and its outer wall is cutinized at maturity.

The endothecium is generally single layered in all the investigated Solanaceae except Nicotiana tabacum and N. glutinosa (Jos and Singh, 1968) and Solanum triquetrum (Ahmad and Siddiqui, 1981) where it is single to multilayered. The fibrous thickenings generally develop in the endothecium except in genera with porous dehiscence (See Davis, 1966). In Solanum nigrum (Saxena and Singh, 1969a) the endothecium persists and fibrous thickenings develop only in the apical region, but in Solanum tuberosum (Young, 1923), S. macranthum (Mohan, 1970) and S. triquetrum (Ahmad and Siddiqui, 1981) the endothecial cells are devoid of fibrillar thickenings.

The innermost layer of the parietal tissue differentiates as the glandular tapetum in Solanum tuberosum (Young, 1923), Lycium europaeum (Jain, 1956), Capsicum frutescens (Lengel, 1960), Withania somnifera (Ram and Kamini, 1964) and Nicotiana tabacum, N. rustica, N. alata, N. glutinosa, N. glauca, N. megalosiphon, N. trigonophylla, N. longiflora and N. plumbaginifolia (Jos and Singh, 1968), Solanum nigrum, S. americanum, S. nodiflorum, S. luteum, S. saracholdes and S. villosum (Saxena and Singh, 1969b). According to Prasad and Singh (1978) the tapetum in Nicandra physaloides degenerates during gametogenesis. Its nuclei fuse to form large polyploid masses before finally collapsing. Ubisch granules are observed. Endomitosis has been

described in the tapetal cells of Lycopersicon esculentum (Brown, 1949), Solanum nigrum and S. dulcamara (Turala and Worytkiewicz, 1964). However, Rybchenko (1963a), who examined the tapetum in 20 species of Solanaceae did not observe endomitosis. An amoeboid tapetum has been reported in Datura stramonium (See Varghese, 1967).

The hypodermal archesporium is generally 1-layered. Young (1923) has described a two layered horse-shoe-shaped archesporium in Datura stramonium. The microspore mother cells undergo usual meiotic divisions. The microspore tetrads are generally tetrahedral in Solanum tuberosum (Khan, 1951), Withania somnifera (Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), Solanum nigrum, S.americanum, S. nodiflorum, S. luteum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) and S. triquetrum (Ahmad and Siddiqui, 1981). The rhomboidal microspore tetrads rare-ly occur in S. triquetrum (Ahmad and Siddiqui, 1981). Sometimes the microspores in a tetrad may be arranged in a linear fashion in S. tuberosum (Khan, 1951). The pollen grains are usually uninucleate, rarely binucleate, at anthesis (Barnard, 1949), while in Lycium europaeum (Jain, 1956), Withania somnifera (Ram and Kamini, 1964), S. nigrum, S. nodiflorum, S. americanum, S. luteum and S. villosum (Saxena and Singh, 1969b), Nicotiana (Jos and Singh, 1968) and S. triquetrum (Ahmad and Siddiqui, 1981) the pollen grains are usually 2-celled at shedding stage. However, in Nicotiana (Podubnaja-Arnoldi, 1936) and Capsi-

cum frutescens (Lengel, 1960) the pollen grains may occasionally be 3-celled.

Erdtman (1952) reviewed the earlier literature on the palynology of Solanaceae. Nair (1965) has described the pollen grains in Atropa belladona, Datura metel, D. stramonium, D. suaveolens, Hyoscyamus niger, Nicandra physaloides, S. pseudocapsicum and S. verbascifolium. The pollen morphology of 93 species belonging to 28 genera of the family has been described by Basak (1967).

Gbile and Sowunmi (1976) studied the pollen morpholog y of Nigerian Solanum species. According to them the pollen grains of 19 taxa of Nigerian Solanum were found to have very similar apertural status, i.e. 3 colporate, the colpi and ora characteristics also being generally similar. The exine pattern is similar, though there are differences in the degree of distinctiveness. There are major differences in overall size and shape. The pollen morphological features are sufficiently distinct to permit the identification of the various species, subspecies and varieties.

The pollen grains of Solanaceae are 3-5 (-6) colpate, colporidate, rarely non aperturate (See Varghese,1967). In Lycium europaeum (Jain, 1956) and Withania somnifera (Ram and Kamini, 1964) and Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S.villosum (Saxena and Singh, 1969b), the pollen grains are tricolpate, spheroidal and having smooth exine. In Nicotiana(Jos and Singh, 1968) the mature pollen grains are globular in shape with

smooth exine and intine and have four germ pores.

The diameter of the pollen grains varies slightly in different species of Nicotiana. The pollen grains in Nicotiana tabacum, N. glutinosa, N. longiflora and N. plumbaginifolia (Jos and Singh, 1968) measure 29 μ in diameter, while in N. rustica, N. glauca and N. alata (Jos and Singj, 1968) they measure about 36 μ. The pollen grains in N. megalosiphon (Jos and Singh, 1968) are the largest and measure about 42 u in diameter.

Krishnamurty and Appa Rao (1958) described polysiphonous germination and branched pollen tubes in hybrids of N. longifolia x N. alata. Vasil (1964) described pollen germination of Capsicum annuum, Solanum melongena and S. tuberosum. Lunyeva, Podubnaja-Arnoldi and Bhaduri (1970) made cytological and histochemical investigations on Nicotiana alata, N. glauca and their hybrid. They recorded considerable meiotic irregularities and a very high percentage of pollen sterility in F_1 hybrids. According to them the mature pollen grains in Nicotiana have polyphenol oxidase while cytochrome oxidase is absent.

Namikawa (1919) described the anther dehiscence in 10 species of Solanaceae. He observed the formation of resorption tissue at the site of dehiscence. Singh and Saxena (1968) have described the method of dehiscence in 20 species belonging to 7 genera of the family. They reported the presence of a resorption tissue in Lycopersicon, Lycium, Capsicum, Physalis and Solanum but a distinct

resorption tissue is not observed in Nicandra. According to Saxena and Singh (1969b) in Solanum nigrum, S. americanum, S. nodiflorum, S. luteum, S. sarachoides and S. villosum the anther dehisces longitudinally and at the site of dehiscence characteristic resorption tissue, resorption cavity, resorption passage and a stomium are organized. However, in Solanum tuberosum (Young,1923),S. triquetrum (Husain, 1968) and S. macranthum (Mohan, 1970) the dehiscence of the anther is porous.

MEGASPORANGIUM, MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

The ovules are anatropous in Nicotiana rustica, N. tabacum and Datura stramonium (Chatin, 1874),Lycopersicum esculentum (Cooper, 1931), S. tuberosum (Rees—— Leonard, 1935), Nicotiana plumbaginifolia and Petunia nyctaginiflora (Bhaduri, 1935), Pepper (Cochran, 1938), Solanum Section Tuberarium (Walker, 1955), Lycium europaeum(Jain, 1956), S. phureja (Dnyansagar and Cooper,1960), Browallia demissa (Mohan, 1966), Nicotiana glutinosa, N. glauca, N. longiflora, N. megalosiphon, N. trigonophylla and N. alata (Jos and Singh, 1968) and Solanum khasianum (Khan and Siddiqui, 1981). The ovule in Solanum tuberosum(Young, 1923) is not, however, of the typical anatropous type, since the embryo sac is considerably curved, suggesting a transition to the campylotropous form. Rees-Leonard (1935) described the amphitropous ovules in S. tuberosum. In Cestrum (Bhaduri, 1935) the ovules are perfectly campylotropous. In Solanum nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena

and Singh, 1969b) the ovules are generally anacampylotropous.

Hemianatropous ovules have been described in Brunfelsia americana, Datura fastuosa, Lycopersicon esculentum, Physalis minima, P. peruviana, Salpiglossis sinuata, Solanum nigrum and Withania somnifera (Bhaduri,1935)and Solanum triquetrum (Ahmad and Siddiqui, 1981).

The female archesporium is generally 1-celled(Schnarf, 1931; Davis, 1966). However, multicellular archesporium is characteristic of Datura (Glisic, 1928; Avery et al,1959) and Solanum tuberosum (Rees-Leonard, 1935).Rarely 2-celled archesporium may occur in Solanum melongena(Bhaduri,1932), S. nigrum, S. americanum, S. luteum, S. nodiflorum and S. garachoidos (Saxena and Singh, 1969b) and S.macranthum (Mohan, 1970), whereas the occurrence of 2-celled archesporium is common in S. villosum (Saxena and Singh,1969b). Multicellular archesporium also may occur in S. melongena (Bhaduri, 1932), Lycopersicum esculentum, Physalis peruviana, Nicotiana plumbaginifolia, Salpiglossis sinuata and Brunfelsia americana (Bhaduri, 1935), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan and Siddiqui, 1981).

The megaspore tetrads are generally linear in Solanum melongena (Bhaduri, 1932), Lycopersicum esculentum(Cooper, 1931), Solanum nigrum, Physalis minima, P. peruviana, W. somnifera, Datura fastuosa, Petunia nyctaginiflora (Bhaduri, 1935), Lycium europaeum (Jain, 1956), Browallia de-

missa (Mohan, 1966), Nicotiana (Jos and Singh, 1968), S. macranthum (Mohan, 1970), Nicandra physaloides (Prasad and Singh, 1978), S. triquetrum (Ahmad and Siddiqui, 1981). The two linear megaspore tetrads lying side by side have been observed in Brunfelsia (Bhaduri, 1935).

The earliest contribution on the development of female gametophyte in Solanaceae is the work of Hofmeister (1958) who observed a mature embryo sac in Hyoscyamus orientalis, Scopolina atropoides and Salpiglossis picta. Polygonum type of embryo sac development has been recorded in Cestrum splendens and Nicotiana tabacum (Guignard, 1882), Atropa belladona (Soueges, 1907), Nicotiana (Palm, 1922), Delitabac and Hyoscyamus niger (Svensson, 1926), Lycopersicum esculentum (Cooper, 1931), Capsicum annuum (Banerji, 1931), S. melongena (Bhaduri, 1932) and S. nigrum (Saxena and Singh, 1969a), Nicotiana rustica (Persidsky and Modilewski, 1935-37), Duboisia liechhardtii, D. myoporoides (Barnard, 1949), Lycium europaeum (Jain, 1956), N. tabacum, N. rustica, N. glutinosa, N. glauca, N. megalosiphon, N. trigonophylla, N. plumbaginifolia, N. longiflora and N. alata (Jos and Singh, 1968), S. macranthum (Mohan, 1970), Withania somnifera (Bhaduri, 1935; Ram and Kamini, 1964; Ariz et al., 1972), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan and Siddiqui, 1981). Longel (1960) described bisporic embryo sac in Capsicum frutescens var. Japanese variegated ornamental, whereas Mutafjan (1964) described monosporic type of embryo sac development in Capsicum. The

Allium type of embryo sac occurs in Capsicum frutescens, Cestrum elegans, Nicotiana ditagla and N. rustica (See Davis, 1966). Nanetti (1912) and Young (1923) found Lilium type of embryo sac and as pointed out by Ram and Kamini (1964) this variation refers to the modern Adoxa type. Modilewski (1935) reported Scilla type of embryo sac development in Nicotiana glauca.

The occurrence of twin embryo sacs in the same ovule has been observed in Solanum tuberosum (Young, 1922), S. melongena (Bhaduri, 1932), Withania somnifera and Physalis minima (Banerji and Bhaduri, 1933), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b).

The synergids are elongated, pyriform and hooked in Solanum phureja (See Davis, 1966) and exhibit filiform apparatus in Lycopersicum esculentum (Cooper, 1931) and S. tuberosum (Rees-Leonard, 1935). Svensson (1926) and Young (1923), however, have not described the occurrence of filiform apparatus in Hyoscyamus niger and S. tuberosum respectively.

The antipodals are usually ephemeral. However, they enlarge and persist during endosperm formation in Atropa belladona, Datura metel and S. phureja (See Davis, 1966). A case of inversion of the embryo sac with a characteristic egg apparatus at the chalazal end has been noted in Lycium europaeum (Jain 1956), Nicotiana (Goodspeed, 1947). This embryo sac has three antipodal like cells at the

micropylar end. In Lycopersicum and Datura (Bhaduri,1935) the two lower antipodals are long and rectangular and fit in the chalazal end of the embryo sac, while the third antipodal is comparatively broader and lie above the two. In Cestrum (Bhaduri, 1935) the two antipodals have been found to be above a broad basal antipodal cell. According to Schnarf (1931) the antipodals are big in S. dulcamara, Atropa belladona and N. tabacum.In Hyoscyamus niger (Svensson, 1926) and Datura laevis (Bhaduri, 1935), the antipodals are small and degenerate early. In Datura metel (Bhaduri, 1935) they persist long after fertilization. In Lycopersicum, Datura and Nicotiana (Bhaduri, 1935) the antipodals could be seen after fertilization. Soueges (1907) believes that the chalazal groove of the embryo sac is a haustorium and the antipodal cells act as secretary organs, which actively secrete chemical substances and help in digesting the nucellar tissue.

FERTILIZATION

The entry of the pollen tube into the ovule is porogamous in Solanum nigrum (Saxena and Singh, 1969a) and Nicandra physaloides (Prasad and Singh, 1978).Double fertilization has been observed in Petunia (Cooper, 1946),S. tuberosum var. chippewa (Williams, 1955) and S. nigrum (Saxena and Singh, 1969a). According to Cooper(1946) fertilization occurs 24 hours after pollination in ovules situated at the top of the ovary while the basal ones are fertilized 32 hours after pollination.

ENDOSPERM

Hofmeister (1958) studied the development of endosperm in Hyoscyamus orientalis, Salpiglossis and Scopolia atropoides and regarded it to be Nuclear type. Nuclear type of endosperm has been reported in Schizanthus pinnatus (Samuelsson, 1913)and Dahlgren, 1923), Capsicum (Crete, 1961c; Mutafjan, 1964) and Solanum triquetrum (Ahmad and Siddiqui 1981).

The Cellular endosperm is of common occurrence and has been described in Atropa, Datura, Physochlaena,Salpiglossis variabilis and Scopolia (Dahlgren, 1923), Petunia (Cooper, 1946), Solanum (Wangenheim, 1957), S. phureja (Dnyan-sagar and Cooper, 1960), Withania somnifera (Ram and Kamini,1964), Nicotiana (Jos and Singh, 1968), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan,1970) and S. khasianum (Khan and Siddiqui, 1981). Svensson (1926) reported ab initio Cellular endosperm in 22 members of Solanaceae. In Hyoscyamus niger he observed Cellular as well as Helobial types.

Ferguson (1927) reported that in Petunia seondary nucleus divides to form a diploid endosperm tissue.Bhaduri (1933) observed this phenomenon in Lycopersicum esculentum and Petunia nyctaginiflora.

The first division of endosperm nucleus is transverse in Datura laevis (Guignard, 1902), Petunia nyctaginiflora (Cooper, 1946), Withania somnifera (Ram and Kamini, 1964), N. tabacum (Jos and Singh, 1968) and S. macranthum(Mohan , 1970). The second division in both the endosperm chambers

is transverse producing four cells arranged linearly. In S. phureja (Dnyansagar and Cooper, 1960) the first two divisions are vertical resulting in the formation of four large cylindrical cells which are of similar dimensions.

The Helobial type of endosperm development has been recorded in Hyoscyamus niger (Svensson, 1926) and Duboisia (See Davis, 1966). The first division of primary endosperm nucleus results in the formation of micropylar and chalazal endosperm chambers of which the micropylar chamber is usually much larger than the chalazal one. The subsequent divisions are free nuclear, so the Helobial type of endosperm is intermediate between the Nuclear and the Cellular types.

The presence of chalazal haustorium has been recorded in S. melongena (Magtang, 1936) and S. phureja (Dnyansagar and Cooper, 1960). In S. macranthum Mohan (1970) recorded that the cells at the two extreme ends ultimately form the chalazal and micropylar haustoria, while the remaining cells give rise to the main body of endosperm.

EMBRYOGENY

The embryogeny in the investigated Solanaceae viz., S. tuberosum, Datura stramonium, Physalis edulis and Atropa belladona (Tognini, 1900), Nicotiana, Datura and Atropa (Souegos, 1920-22b), N. rustica (Persidisky and Modilewski, 1935; Modilewski, 1937), Physalis minima, Withania somnifera and Petunia nyctaginiflora (Bhaduri, 1936), Schizanthus and Petunia (Soueges, 1936), Physalis

peruviana (Crete, 1954), S. demissum (Walker,1955),Saracha jaltomato (Crete, 1960), S. phureja (Dnyansagar and Cooper, 1960), Datura tatula (Crete, 1961a), Browallia demissa (Crete, 1961b), Salpiglossis sinuata (Crete, 1961d), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. saracholdes and S. villosum (Saxena and Singh, 1969b), S. triquetrum (Ahmad and Siddiqui, 1981) conforms to the Nicotiana variation of the Solanad type. However, in Capsicum annuum (Crete, 1961c) the development follows Onagrad type.

The phenomenon of polyembryony has been reported by Biraghi (1929), who observed the formation of adventitious embryos in Nicotiana rustica var. Brasilie when pollinated with Petunia pollen. Haberlandt (1931) observed parthenogenetic development of the endosperm and early stages in the development of adventitious embryos in Scopolia. Polyembryony has also been reported by Banerji and Bhaduri (1933) in Nicotiana plumbaginifolia, Withania somnifera and Petunia nyctaginiflora. According to them (1933) two well developed embryos have been found in two separate embryo sacs in the same ovule in Nicotiana plumbaginifolia. Banerji and Bhaduri (1933) observed earlier stages of development of adventitious embryos by budding of the nucellar cells covering the embryo sac in Petunia nyctaginiflora and Withania somnifera. Cooper (1943) observed haploid seedlings during his course of investigation on interspecific hybridization of Nicotiana. This made him

to suggest that one embryo developed from the synergid and was haploid in origin. A case of polyembryony in N. tabacum giving rise to two seedlings with different chromosome numbers has been reported by Cameron (1949).

SEED

Netolitzky (1926) described the structure and development of seed in Solanaceae. The most outstanding and exhaustive study of the seed coat anatomy of 146 species belonging to 26 genera of the Solanaceae has been made by Soueges (1907). According to him the fully mature integument is differentiated into the following 3 zone of which the middle one is divided into two:

(i) Assise externe: the outer epidermis

(ii) Assise interne: the inner epidermis

(iii) Partie moyene : the intermediate layer of cells which consists of two zones.

(a) Zone externe

(b) Zone interne

The layers comprising partie moyene lose their contents and mostly disintegrate. Only a few outermost layers persist in seeds in greatly compressed form. On the basis of this histological differentiation of these three layers, Soueges (1907) has been able to classify the principal genera under Solanaceae.

Smith (1935) and Cochran (1938) gave detailed account of the development and structure of seed in Lycopersicum esculentum and Capsicum frutescens var. grossus respec-

tively. Similar studies have been made by Barnard (1949), Dnyansagar and Cooper (1960), Jain (1962) and Czaja(1963, 1965).

In S. nigrum (Saxena and Singh, 1969a), S. macranthum (Mohan, 1970) and Micandra physaloides (Prasad and Singh, 1978) the seed coat consists of 4 or 5 layers including the persistent endothelium, while in S. nigrum, S. americanum, S. lutoum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b) the seed coat consists of an epidermis and a persistent endothelium. The size and shape of the endothelial cells and the nature of thickenings on their walls vary in different species of Solanums.

The seed coat may or may not be multiplicative, generally reduced to the epidermis and the endothelium. The epidermis is compact layer of cells with more or less undulate or stellate facets, either with more or less strongly thickened inner and radial walls in Atropa, Browallia, Cestrum, Lycium, Mandragora, Micandra, Nicotiana, Petunia, Solanum and Withania (See Corner, 1976).

EXTERNAL MORPHOLOGY

SOLANUM HISPIDUM PERS.

Solanum hispidum is a perennial prickly shrub about 2-2.5 m high clothed with ferrugineous stellate tomentum. The leaves are 10-20 cm long, ovate, sinuate or coarsely lobed, stellate-tomentose and somewhat rough above, ferrugineous tomentose below, with a few prickles on the mid rib; petiole 1-2.5 cm long.

The inflorescence is extra-axillary ferrugineous tomentose cyme. The flower is pedicellate, ebracteate, complete, bisexual, actinomorphic, hypogynous and pentamerous. Occasionally the flowers may be tetramerous to decamerous.

The calyx lobes are gamosepalous bell-shaped, persistent. The corolla is five lobed, gamopetalous, campanulate and measures about 2.0 cm diameter, white in colour.

The stamens are five, polyandrous, epipetalous, filament short, anthers bilobed, basifixed with porous as well as longitudinal dehiscence.

The ovary is bicarpellary, syncarpous superior, bilocular with swollen axile placente. Style is long with lobed stigma. Heterostyly frequently occur.

The fruit is a berry, globose and measures about 1.5 cm diameter.

Solanum hispidum

SOLANUM FURCATUM DUN.

Solanum furcatum is an annual herb about 80-100 cm long. The stem is erect, branched, herbaceous, solid, angular with trichomes. The leaves are large, petiolate (1.25-1.5 cm) long, exstipulate, cordate, serrate margin with acute apex. The texture of leaf is herbaceous and hairy. The leaves are 4-6 cm long with reticulate unicostate venation.

The inflorescence is extra axillary cyme. The flower is pedicellate (0.8-1.0 cm long), ebracteate, complete, bisexual, actinomorphic, hypogynous and pentamerous. The flower measures 0.5 cm long.

The calyx lobes are gamesepalous bell-shaped, persistent, each lobe measures 0.2 cm long. The corolla is 5 lobed, gamopetalous, campanulate and measures 0.3-0.4 cm long.

The stamens are five in number, polyandrous, epipetalous, filament 0.4 cm long. Anthers bilobed, basifixed with porous dehiscence.

The ovary is bicarpellary syncarpous, superior, bilocular with swollen axile placenta. The length of style is 0.5 cm. The base of the style is feathery, stigma is capitate.

The fruit is berry, dull bluish black in colour.

SOLANUM RETROFLEXUM DUN.

Solanum retroflexum is an annual herb, 45-60 cm long. The stem is erect, profusely branched, solid, cylindrical and hairy.

The leaves are petiolate, petiole 0.5-1.0 cm long, exstipulate, alternate, cordate with serrate margin, acute apex and hairy surface. Texture is herbaceous. The length of leaf is 2.5 cm. Leaves are simple, broad at the base with reticulate unicostate venation.

The inflorescence is extra axillary cyme. The flowers are pedicellate (0.6 cm long), ebracteate, bisexual, complete, actinomorphic, hypogynous, pentamerous and white in colour.

The calyx is five lobed, gamosepalous, bell-shaped 0.2 cm long, green in colour, persistent. The corolla is five lobed, gamopetalous 0.5 cm long.

The stamens are five, epipetalous, polyandrous, anthers basifixed, filament is 0.3 cm long. The dehiscence of the anther is porous.

The ovary is superior, bicarpellary, syncarpous, bilocular with many ovules in each locule with swollen axile placenta. Style is 0.3 cm long and feathery at the base. Stigma is capitate.

The fruit is berry, dull bluish black in colour.

Solanum retroflexum

SOLANUM DOUGLASII DUN.

Solanum douglasii is an annual herb measuring 1.25-1.5 meter, erect, branched, herbaceous, solid, angular, the edges are dentate and hairy.

The leeves are simple, petiolate 1.0 cm long, exstipulate, alternate, ovate in shape with entire margin and acute apex. The leaf is 3-6 cm long, shows herbaceous texture with reticulate unicostate venation.

The inflorescence is extra axillary cyme. The flower is pedicellate (0.8 cm long), ebracteate, complete, bisexual, actinomorphic, hypogynous, white in colour.

The calyx lobes are five in number, gamosepalous bell-shaped, persistent 0.3 cm long. Five corolla lobes are gamopetalous. The petals measure 0.6 cm long, campanulate.

The stemans are five in number, polyandrous, epipetalous, filament 0.4 cm long, anthers basifixed and bilobed. The dehiscence of the anther is porous.

The ovary is superior, bicarpellary, syncarpous, bilocular with many ovules in each locule and with swollen axile placenta. The base of the stigma is feathery. The stigma is capitate.

The fruit is berry, shining bluish black in colour.

Solanum douglasii

SOLANUM CORNUTUM LAM.

Solanum cornutum is prickly bright green annual herb measuring 40-47 cm high. The stem is erect, herbaceous but woody at the base, branched, solid and cylindrical with shining yellow prickles upto 0.5 cm long.

The leaves are ramal and cauline, alternate, petiolate (2.0-3.0 cm long), exstipulate, subpinnatifid, ovate, covered with glandular hairs, reticulate unicostate venation armed with long straight yellow spines.

The inflorescence is extra axillary peduncled cyme. The flower is pedicellate (0.6 cm long), ebracteate, complete, bisexual, zygomorphic, pentamerous, bluish purple in colour.

The calyx lobes are five (0.5 cm long), gamosepalous, lanceolate, acute apex, densely hairy and prickly at the base, persistent and accrescent. The corolla is five lobed, gamopetalous, funnel shaped and about 1.5cm long. The corolla is zygomorphic, two petals are broad and long while the remaining three are small and narrow.

The androecium consists of five epipetalous stamens. Heteroanthy has been observed. One of the stamens is considerably long (1.2 cm) and petaloid while the remaining ones are short and of equal size. The filament is 1.0 cm long. The anthers are sagittate, basifixed and bithecous. The dehiscence of the anther is porous as well as by means of small pores formed at intervals in the longitudinal suture.

The ovary is superior, bicarpellary syncarpous and

bilocular with swollen axile placenta. The style is considerably long (1.7 cm)with capitate stigma.

The fruit is berry, brownish balck in colour.

Solanum cornutum

FLORAL ORGANOGENY

The floral parts differentiate in acropetal succession in Solanum hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum.

The floral primordium arises as a small rounded mass of cells (Fig. 1), which soon becomes broad and somewhat flattened at the top. In a median longitudinal section of the flower bud the calyx lobes are seen as small outgrowths on each side of the convex floral axis (Fig. 2). The calyx develops considerably before the differentiation of other floral structures enclosing the convex receptacle. Next to the calyx primordia the rudiments of corolla arise (Figs. 3, 4). The corolla is much thinner than the calyx and grows more rapidly. The growth of the corolla is less upright than that of the calyx and the margin becomes somewhat incurved.

Soon after the initiation of corolla lobes the primordia of the stamens arise (Fig. 5). Very soon the stamen primordium differentiates into a bulbous apex and narrow basal part. The former gives rise to the anther and the latter to the filament (Figs. 6, 7). The anther becomes bilobed by a constriction in the middle (Fig. 8). The floral apex left after the differentiation of the androecium is utilized in the formation of gynoecium. The ovary wall originates as a small outgrowth (Fig. 6). Later this outgrowth forms the ovary wall and the remaining central part gives rise to the placenta (Fig. 7). The ovary wall

continues to grow up converging towards the centre. Soon it covers the placenta completely, straightens and forms a long and solid style. The stigma is papillate (Fig.8).

A transverse section of the flower bud shows five lobes of calyx as a marginal ring, whose ends are fused. The corolla lobes are five in number, alternate with the segments of the calyx. They are somewhat thin and rolled inward at the margins. The stamens alternate with the petals. The anthers are four chambered, each with a central vascular strand (Fig. 9). The pistil is round and consists of two carpels (Fig. 10). The ovules develop in basipetal succession on the entire surface of the placenta.

EXPLANATION OF FIGURES

Figs. 1-10. *Solanum hispidum*. Floral organogeny. Fig. 1. L.s. floral primordium. Fig. 2. L.s. bud showing calyx primordia. Figs. 3, 4. L.s. buds showing initiation of corolla primordia. Fig. 5. L.s. bud showing initiation of androecium. Fig. 6. L.s. bud showing initiation of gynoecium. Figs. 7, 8. L.s. flower buds showing calyx, corolla, stamen and gynoecium. Fig. 9. T.s. flower bud passing through style. Fig. 10. T.s. flower bud passing through ovary. (K=calyx; C=corolla; A=androecium; OW=ovary wall; PL=placenta).

MICROSPORANGIUM

The five epipetalous initials of the stamens arise as blunt processes. These undifferentiated masses of cells soon become bilobed, each lobe bearing a pair of loculi. The anther is basally attached to its filament.

A young anther is quadrangular in transection and consists of parenchymatous cells (Figs. 11, 17, 25, 33, 41). The hypodermal multicellular archesporium differentiates at the four corners of the anther. These cells are densely cytoplasmic and possess prominent nuclei (Figs. 12, 18, 26, 34, 42). The archesporial cells divide periclinally producing an outer primary parietal layer and an inner sporogenous layer (Figs. 19, 27, 35). The cells of the latter enlarge and divide mitotically forming a large number of microspore mother cells. The primary parietal layer undergoes a periclinal division forming an outer and inner secondary parietal layers (Figs. 20, 28, 36, 43, 44). The inner secondary parietal layer directly differentiates into the tapetum (Figs.13, 14, 21, 29, 37, 45), while the outer secondary parietal layer divides again periclinally producing two layers of cells, of which the outer differentiates as endothecium and the inner as the middle layer. Thus the development of the anther wall layers corresponds to the Dicotyledonous type of Davis (1966).

The epidermal cells of a mature anther are tangentially elongated (Figs. 15, 16, 22, 23, 30, 31, 38, 39,

46, 47). The outer tangential walls bear thin cuticular thickenings in S. hispidum and S. douglasii (Figs.16,39). The protoplast of epidermal cells shrinks at the shedding stage of the pollen grains.

The hypodermal endothecium is single layered in S. furcatum and S. douglasii (Figs. 22, 38), 2-layered in S. retroflexum (Fig. 30), 4-layered in S. hispidum (Fig. 15) and 2-4-layered in S. cornutum (Figs. 46, 47). The endothecium is devoid of fibrous thickenings. It persists and develops fibrous thickenings only in the apical region in S. furcatum, S. retroflexum and S. douglasii (Figs. 24, 32, 40).

Next to the endothecium is the middle layer, which consists of a strip of very narrow cells. In S. retroflexum there is single middle layer (Fig. 30). There are two middle layers in S. hispidum and S. furcatum (Figs. 15, 22), three middle layers in S. douglasii (Fig. 38) and 2-4 middle layers in S. cornutum (Figs. 46,47). The middle layers are sandwitched between the endothecium and the tapetum. As a rule middle layers get crushed and absorbed during the development of pollen grains.

The innermost layer of the parietal tissue differentiates as the glandular tapetum. The tapetal cells possess vacuolated cytoplasm at microspore mother cells stage. The tapetal nuclei divide mitotically and the tapetal cells become binucleate (Figs. 15, 22, 30, 38,46, 47). At places the tapetal cells may have 2-4 nuclei in S. furcatum and S. cornutum (Figs. 22, 46-49). Later,the

tapetal cells enlarge and the cytoplasm becomes vacuolated. The vacuoles in S. hispidum are towards the sporogenous layer (Fig. 15), while in S. douglasii these are towards the middle layers (Fig. 38). The tapetum is absorbed during the formation and maturation of the pollen grains.

The dehiscence of the anther is porous in S.furcatum, S. retroflexum and S. douglasii and porous as well as longitudinal in S. hispidum. In S. cornutum, the dehiscence is porous as well as with the help of pores formed, at different intervals in the longitudinal suture. Some hypodermal cells differentiate in the septal region between the adjacent pollen sacs at the mature pollen grain stage in S. hispidum and S. cornutum. The cells are larger than the adjoining cells and form the resorption tissue. During later development their nuclei and cell walls disintegrate and a lysigenous cavity is thus formed. The process of lysis continues till most of the adjacent parenchyma is consumed forming a passage between the pollen sacs of an anther lobe (Fig.50). The resorption passage broadens as the septum collapses. Simultaneously, the stomium differentiates in the epidermis opposite the resorption passage (Fig. 51). The cells of the stomium soon disjoin and the anther wall splits forming a longitudinal slit. The dehiscence slit runs upto the tip of the anther lobes.

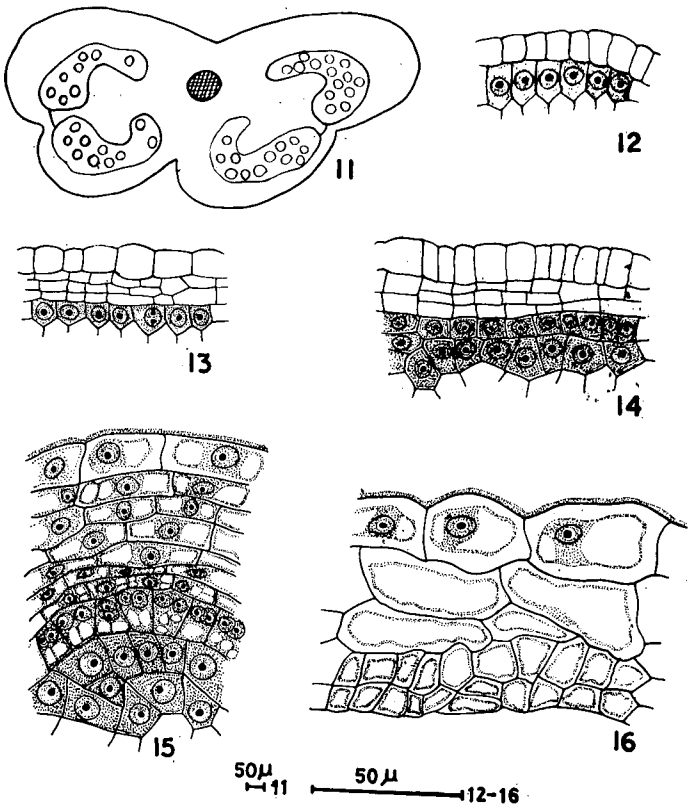
MICROSPORANGIUM

DISTINGUISHING FEATURES

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Microsporangium	4-chambered	4-chambered	4-chambered	4-chambered	4-chambered
Anther wall development	Dicotyledonous	Dicotyledonous	Dicotyledonous	Dicotyledonous	Dicotyledonous
Epidermis	Tangentially elongated cells with thin cuticular thickenings	Tangentially elongated cells	Tangentially elongated cells	Tangentially elongated cells with thin cuticular thickenings	Tangentially elongated cells
Endothecium	4-layered non fibrous	1-layered fibrous thickenings at tip region	2-layered fibrous thickenings at tip region	1-layered fibrous thickenings at tip region	2-4-layered non fibrous
Middle layers	Two ephemeral	Two ephemeral	One ephemeral	Three ephemeral	Two to four ephemeral
Tapetum	2-nucleate ephemeral	2-4-nucleate ephemeral	2-nucleate ephemeral	2-nucleate ephemeral	2-4-nucleate ephemeral
Dehiscence	Porous as well as longitudinal	Porous	Porous	Porous	Porous as well as by pores in longitudinal suture

EXPLANATION OF FIGURES

Figs. 11-16. *Solanum hispidum*. Microsporangium. Fig. 11. T.s. bithecous anther showing four pollen chambers. Fig. 12. L.s. part of anther showing hypodermal archesporium. Fig. 13. L.s. part anther showing sporogenous and secondary parietal layers. Fig. 14. L.s. part anther showing sporogenous tissue and tapetum. Fig. 15. L.s. part of anther showing structural details of anther wall layers. There are 3-4 layered endothecium, 2 middle layers, binucleate tapetum and sporogenous tissue. Fig. 16. L.s. dehisced anther showing epidermis and 3-4 layered non-fibrous endothecium.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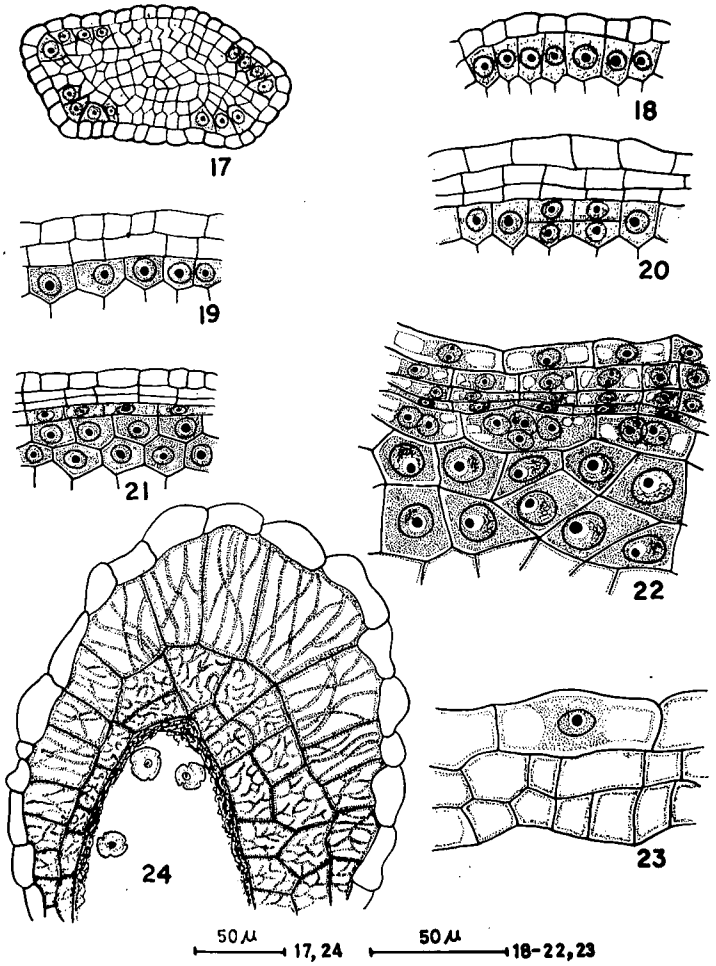
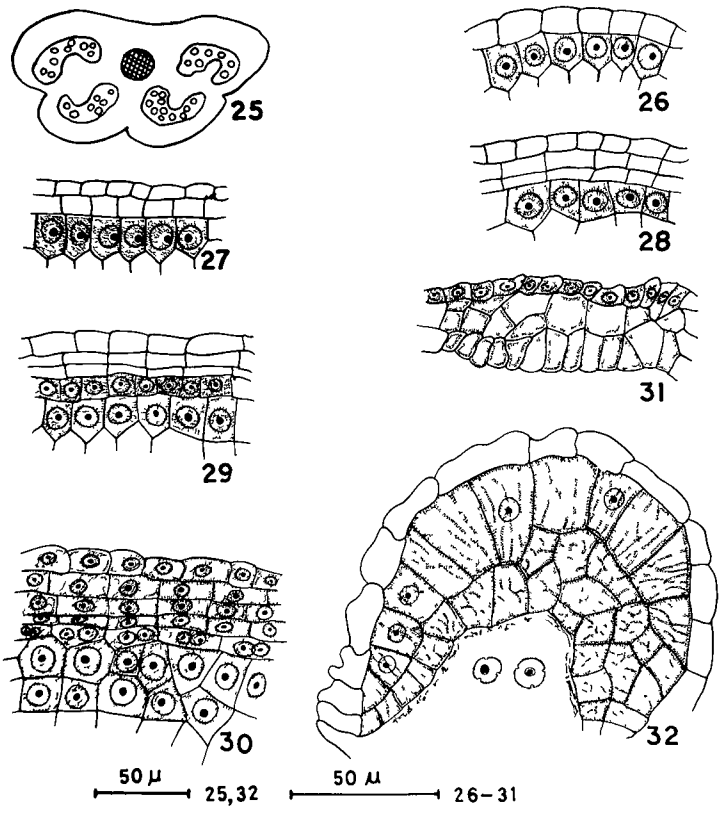
EXPLANATION OF FIGURES

Figs. 17-24. *Solanum furcatum*. Microsporangium. Fig. 17. T.s. anther showing four archesporia. Fig. 18. L.s. part anther showing hypodermal archesporium. Fig. 19. L.s. part anther showing sporogenous and primary parietal layers. Fig. 20. L.s. anther showing sporogenous tissue and secondary parietal layers. Fig. 21. L.s. anther showing, sporogenous tissue, tapetum and initials of endothecium and middle layers. Fig. 22. L.s. anther showing structural details of anther wall layers. Fig. 23. L.s. dehisced anther showing epidermis and 2-layered endothecium. Fig. 24. L.s. anther tip showing epidermis and fibrillar endothecium.


17
18
19
20
21
22
23
24
50 μ
17, 24
50 μ
18-22, 23

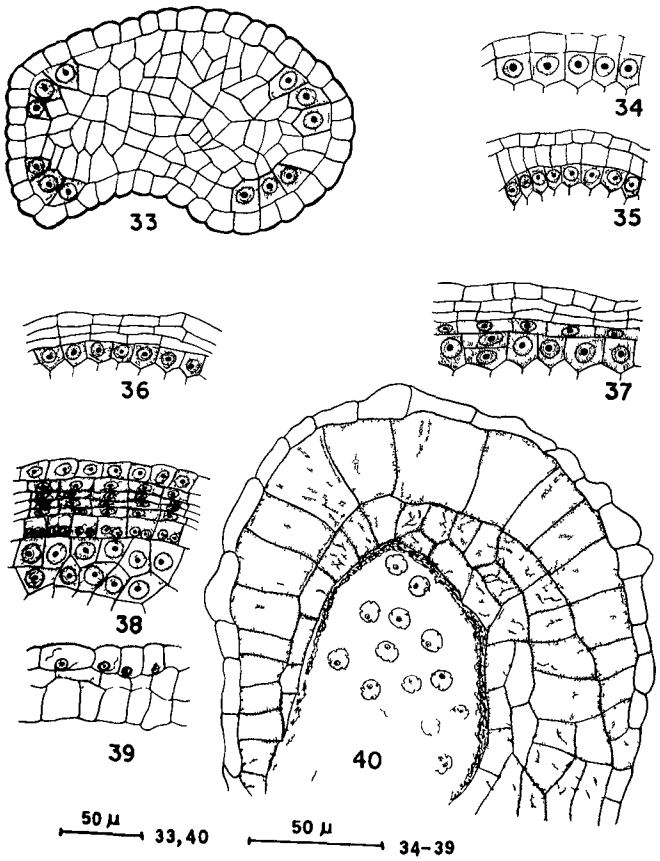
EXPLANATION OF FIGURES

Figs. 25-32. Solenum retroflexum. Microsporangium. Fig. 25. L.s. anther showing four pollen chambers. Fig. 26. L.s. part anther showing hypodermal archesporium. Fig. 27. L.s. part anther showing sporogenous and primary parietal layers. Fig. 20. L.s. part anther showing sporogenous and secondary parietal layers. Fig. 29. L. s. part anther showing sporogenous and tapetal layers and the layers that would develop into endothecium and middle layers. Fig. 30. L.s. anther showing structural details of anther wall layers. Fig. 31. L.s. dehisced anther showing epidermis and 2-3-layered endothecium Fig. 32. L.s. tip of anther showing epidermis and 2-4-layered fibrous endothecium.


25
26
27
28
29
31
30
32
50 µ
25,32
50 µ
26–31

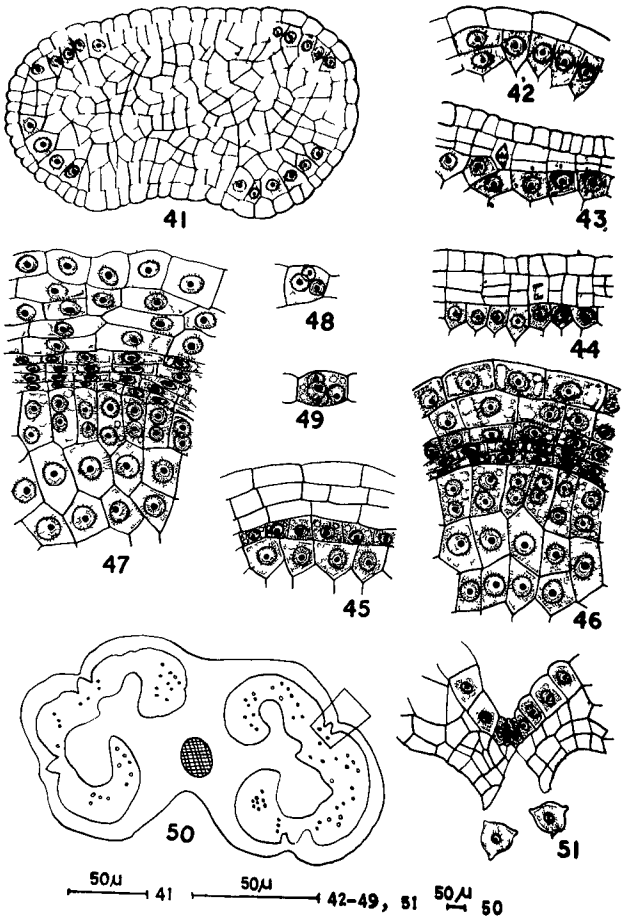
EXPLANATION OF FIGURES

Figs. 33-40. *Solanum douglasii*. Microsporangium. Fig. 33. T.s. anther showing four archesporia. Fig. 34. L.s. part anther showing hypodermal archesporium. Fig. 35. L.s.part anther showing sporogenous and primary parietal layers. Fig. 36. L.s. part anther showing sporogenous and secondary parietal layers. Fig. 37. L.s. part anther showing sporogenous layer, tapetum and layers that would develop into endothecium and middle layers.Fig.38. Structural details of anther wall layers. Fig. 39. L.s. part dehisced anther showing endothecium. Fig. 40. L.s. tip of mature anther showing epidermis and 2-4-layered fibrous endothecium.


33
34
35
36
37
38
39
40
50 µ
33,40
50 µ
34-39

EXPLANATION OF FIGURES

Figs. 41-51. Solanum cornutum. Microsporangium. Fig. 41. T.s. anther showing four archesporia. Fig. 42. L.s. part anther showing hypodermal archesporium. Fig. 43. L.s. part anther showing sporogenous and secondary parietal layers. Fig. 44. L.s. part anther showing sporogenous and secondary parietal layers. Some cells of outer secondary parietal layer have divided. Fig. 45. L.s. part anther showing sporogenous cells, tapetum and two layers that would develop into endothecium and middle layers. Figs. 46, 47. Structural details of anther wall layers. Figs. 48, 49. 3 and 4-nucleate tapetal cells respectively. Fig. 50. T.s. anther showing region of longitudinal dehiscence. Fig. 51. T.s. part anther showing resorption cavity.


41
42
43
44
45
46
47
48
49
50
51
50μ
41
50μ
42-49, 51
50μ
50

MICROSPOROGENESIS

Before the meiotic divisions set in, the protoplast of the microspore mother cell develops a new wall of considerable thickness on the inner side of its original wall, which is mucilaginous in nature and thicker at the angles in all the species described here.

The microspore mother cells undergo meiotic divisions. The divisions in all the mother cells of an anther may not be synchronous. Thus different stages of microsporogenesis may be present in the four chambers of the same anther. The microspore mother cells undergo meiosis, no cell plate is laid down after meiosis I. Cytokinesis takes place after telophase II when the spindle fibres disappear (Figs. 52-57, 64-68, 76-79, 92-96,107-113). Thus cytokinesis is of simultaneous type. Cytokinesis takes place by centripetally advancing constriction furrows which meet at the centre. Soon afterwards the microspores develop their individual walls.

Different types of microspore tetrads result due to the differences in the orientation of the spindles at the second meiotic divisions. Generally the microspore-tetrads are tetrahedral (Figs. 58, 69, 80, 97, 114). Occasionally they may be isobilateral in S. hispidum, S. douglasii and S. cornutum (Figs. 59, 98, 115) and decussate in S. furcatum and S. retroflexum (Figs. 70, 81). Rarely rhomboidal and decussate arrangements have been observed in S. hispidum, S. douglasii and S. cornutum

(Figs. 61, 60, 100, 99, 116, 117). Rarely the microspore tetrads may be isobilateral and rhomboidal in S.furcatum and S. retroflexum (Figs. 71, 72, 82, 83).

MALE GAMETOPHYTE

The wall of the microspore mother cells breaks down and the young microspores are liberated into the anther loculus. The young microspore shows somewhat triangular outline with dense cytoplasm. Later it becomes spherical, possesses vacuolated cytoplasm and develops smooth, transparent and considerably thick exine.

Generally the pollen grains are tricolporate in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum (Figs. 62, 63, 73, 74, 84, 85, 87, 91, 101-106, 116, 121). During further development of male gametophyte the vacuoles disappear and the cytoplasm becomes replete with starch grains in S. hispidum (Figs. 62, 63), S. furcatum (Figs. 73-75) and S. cornutum (Figs. 121, 122). Sometimes in S. cornutum the hilum of the starch grains is not stained properly, and therefore, they appear as small vacuoles in the cytoplasm (Figs. 121, 122).

The division of the microspore nucleus results in a large vegetative and a small generative nucleus (Figs. 63, 74, 85, 121). A small generative cell is organized at one sid of the pollen grain, which is d limited by a hyaline wall (Figs. 86, 102). The generative cell rounds up and finally lies in the cytoplasm of pollen grain. Thus the pollen grains appear to be 2-nucleate in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum (Figs. 63, 74, 87, 103, 121). The gene-

rative cell divides mitotically forming two male gametes, thus the pollen grains become 3-nucleate (Figs. 88, 89, 104, 105). The cytoplasm which surrounds the two male gametes is somewhat different from the general cytoplasm. Thus it appears that the two sperm cells are formed.

Variations in the structure of the pollen grains and behaviour of nuclei have also been observed. Normally the pollen grains are tricolporate, tetracolporate pollen grains have been observed in S. furcatum, S. retroflexum and S. cornutum (Figs. 75, 86, 88, 89, 120) and multicolporate in S. retroflexum (Fig. 90). Sometimes in S. furcatum and S. douglasii the two nuclei may be of equal size (Figs. 75, 106). They could give rise to two gametophytes. In one case in S. retroflexum a 3-nucleate pollen grain shows two big nuclei of equal size while the third one is smaller (Fig. 90). Still in another case in a 3-nucleate pollen grain the size of all the three nuclei are different (Fig. 91). It may be interpretted that the nucleus of the microspore had produced two nuclei of equal size as shown in figures 75 and 106 and one of the two nuclei had divided producing one small and a large nucleus. Sometimes the pollen grains may germinate in situ in S. cornutum (Fig. 119). Generally the germination of pollen grains is monosiphonous, rarely polysiphonous condition has also been observed (Fig. 122).

Pollen grains are shed at 2-nucleate stage in S. hispidum, S. furcatum and S. cornutum (Figs. 63, 74, 121),

while in S. retroflexum and S. douglasii they are shed at 3-nucleate stage (Figs. 89, 105).

Pollen sterility has also been observed. It is more common in S. hispidum. The percentage of fertile pollen grains is approximately 38.32.

Size of the pollen grains varies considerably in the species described here. Average diameter of 20 pollen grains measured is maximum in S. furcatum(23.55 μ) and minimum in S. douglasii (15.675 μ), while in S. hispidum, S. retroflexum and S. cornutum the diameter of the pollen grains is 19.695 μ, 20.175 μ and 17.25 μ respectively.

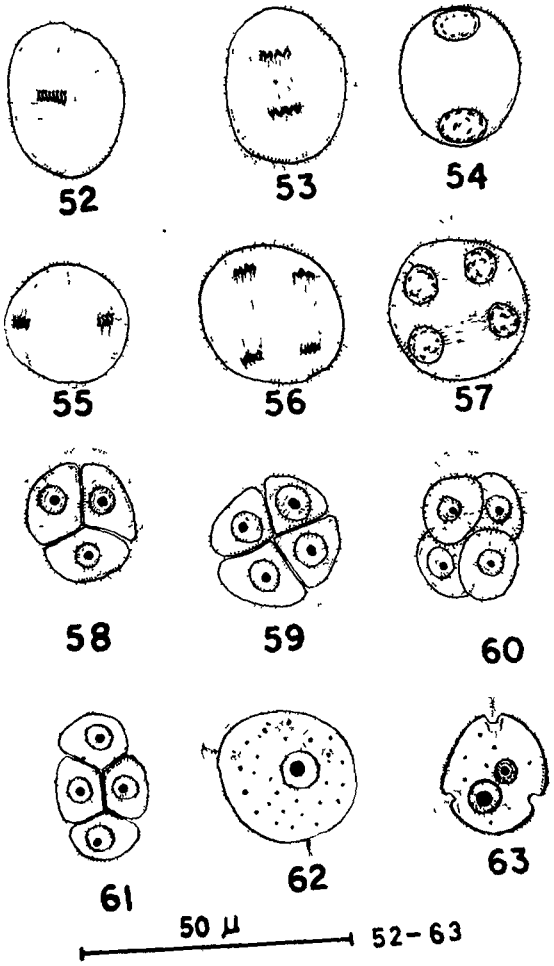
MICROSPOROGENESIS AND MALE GAMETOPHYTE

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Meiotic divisions	Non-synchronous	Non-synchronous	Non-synchronous	Non-synchronous	Non-synchronous
Cytokinesis	Simultaneous	Simultaneous	Simultaneous	Simultaneous	Simultaneous
Microspore tetrads	Tetrahedral Occasionally isobilateral rarely rhomboidal & decussate	Tetrahedral Occasionally decussate rarely isobilateral & rhomboidal	Tetrahedral Occasionally decussate rarely isobilateral & rhomboidal	Tetrahedral Occasionally isobilateral rarely rhomboidal & decussate	Tetrahedral Occasionally isobilateral rarely rhomboidal & decussate
Pollen grain	Tricolporate Exine smooth Starch grain present	Tricolporate Occasionally tetracolporate Exine smooth Starch grain present	Tricolporate Occasionally tetracolporate exceptionally multicolporate Exine smooth Starch grain absent	Tricolporate Exine smooth Starch grain absent	Tricolporate Occasionally tetracolporate Exine smooth Starch grain present
Size of pollen grain	19.69 μ	23.55 μ	20.17 μ	15.67 μ	17.25 μ
Shedding stage	2-nucleate	2-nucleate	3-nucleate	3-nucleate	2-nucleate
Pollen Germination	Monosiphonous	Monosiphonous	Monosiphonous	Monosiphonous	Monosiphonous rarely polysiphonous and *in situ* germination

EXPLANATION OF FIGURES

Figs. 52-63. *Solanum hispidum*. Microsporogenesis and male gametophyte. Figs. 52-57. Microspore mother cells undergoing meiosis. Figs. 58-61. Tetrahedral, isobilateral, decussate and rhomboidal microspore tetrads respectively. Fig. 62. Uninucleate pollen grain. Fig. 63.2-nucleate pollen grain showing large vegetative and a small generative nucleus.


52
53
54
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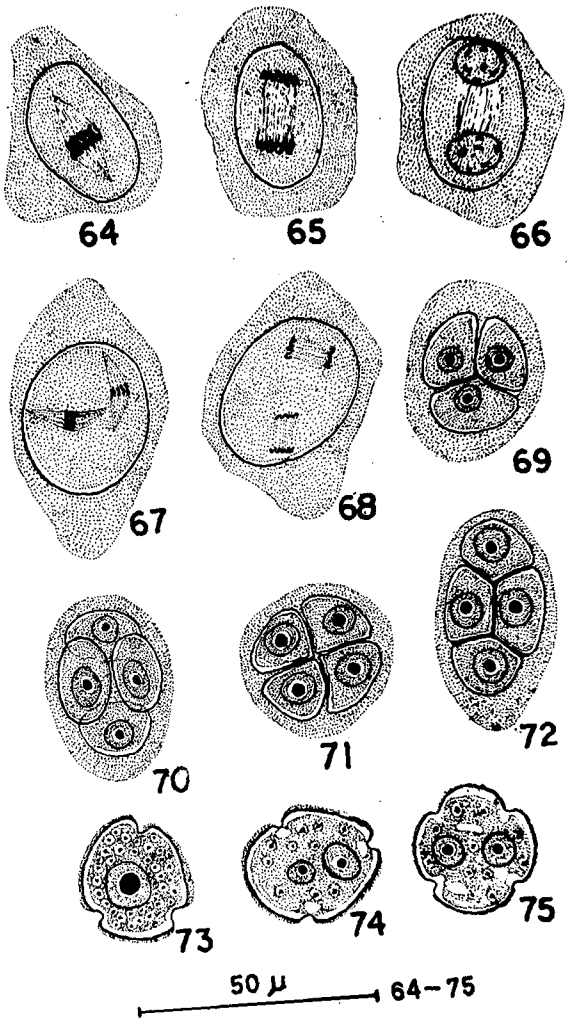
56
57
58
59
60
61
62
63
50 µ
52-63

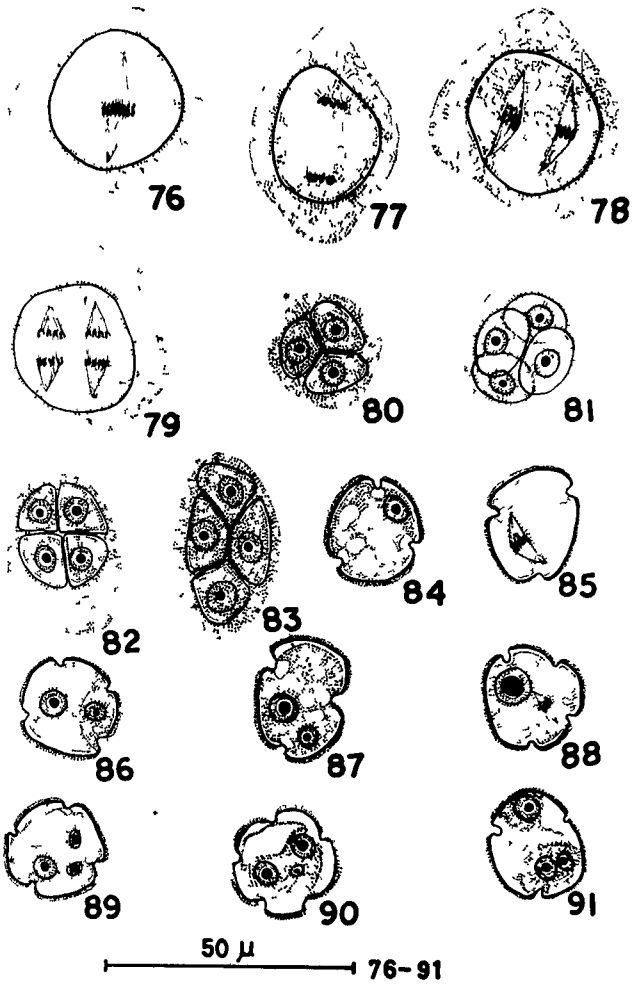
EXPLANATION OF FIGURES

Figs. 64-75. *Solanum furcatum.* Microsporogenesis and male gametophyte. Figs.64-66.Microspore mother cells undergoing first meiotic divisions.Figs.67-68. Microspore mother cells showing second phase of meiosis. Figs. 69-72. Tetrahedral, decussate, isobilateral and rhomboidal microspore tetrads respectively Fig. 73. Uninucleate tricolporate pollen grain showing starch grains. Fig. 74. Binucleate pollen grain. Fig. 75. Tetracolporate pollen grain showing both the nuclei of equal size.


64
65
66
67
68
69
70
71
72
73
74
75
50 μ
64–75

EXPLANATION OF FIGURES

Figs. 76-91. Solanum retroflexum. Microsporogenesis and male gametophyte. Figs. 76, 77. Microspore mother cells showing metaphase I and anaphase I respectively. Figs. 78, 79. Microspore mother cells showing metaphase II and anaphase II respectively. Figs. 80-83. Tetrahedral, decussate, isobilateral and rhomboidal microspore tetrads respectively. Fig. 84. Uninucleate pollen grain showing vacuolated cytoplasm. Fig. 85. Microspore nucleus undergoing first mitotic division. Fig. 86.2-celled pollen grain. Fig. 87. Tricolporate pollen grain with large vegetative and a small generative nucleus. Fig. 88. Tetracolporate 2-nucleus pollen grain. The generative nucleus is dividing. Fig. 89. 3—nucleate pollen grain. Fig. 90. Multicolporate pollen grain with two large and a small nucleus. Fig. 91.3-nucleate pollen grain.


76
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82
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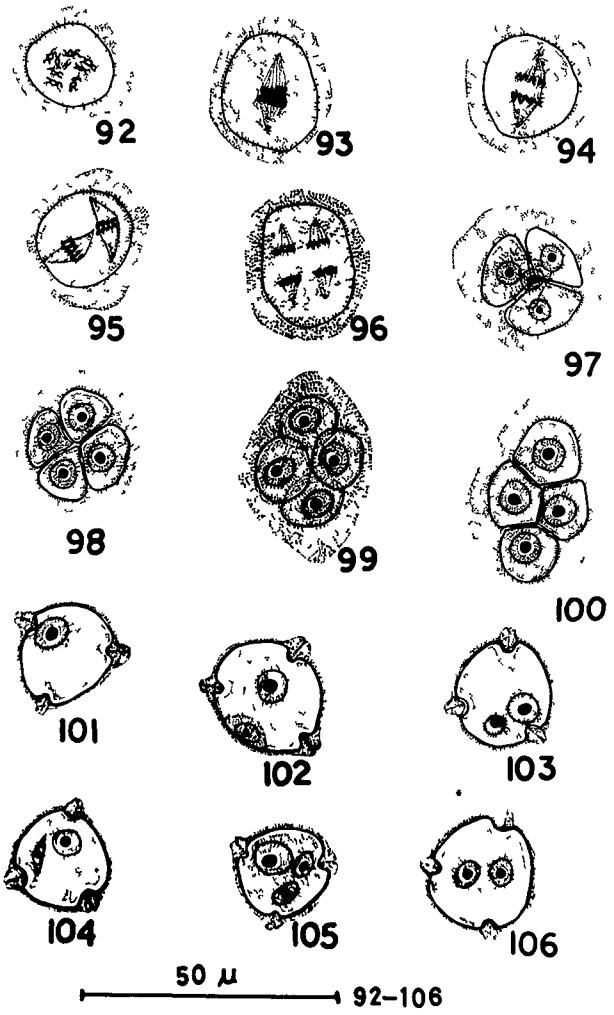
84
85
86
87
88
89
90
91
50 μ
76-91

EXPLANATION OF FIGURES

Figs. 92-106. *Solanum douglasii*. Microsporogenesis and male gametophyte. Figs. 92-94. Microspore mother cells showing diakinesis, metaphase I and anaphase I respectively. Figs. 95, 96. Microspore mother cells showing metaphase II and anaphase II respectively. Figs. 97-100. Tetrahedral, isobilateral, decussate and rhomboidal microspore tetrads respectively. Fig. 101. Uninucleate pollen grain showing large vacuole. Fig. 102. 2-celled pollen grain. Fig. 103. 2-nucleate pollen grain showing a large vegetative and a small generative nucleus. Fig. 104. 2-nucleate pollen grain. The generative nucleus is undergoing mitosis. Fig. 105. 3-nucleate pollen grain. Fig. 106. 2-nucleate pollen grain. Both the nuclei are of equal size.


92
93
94
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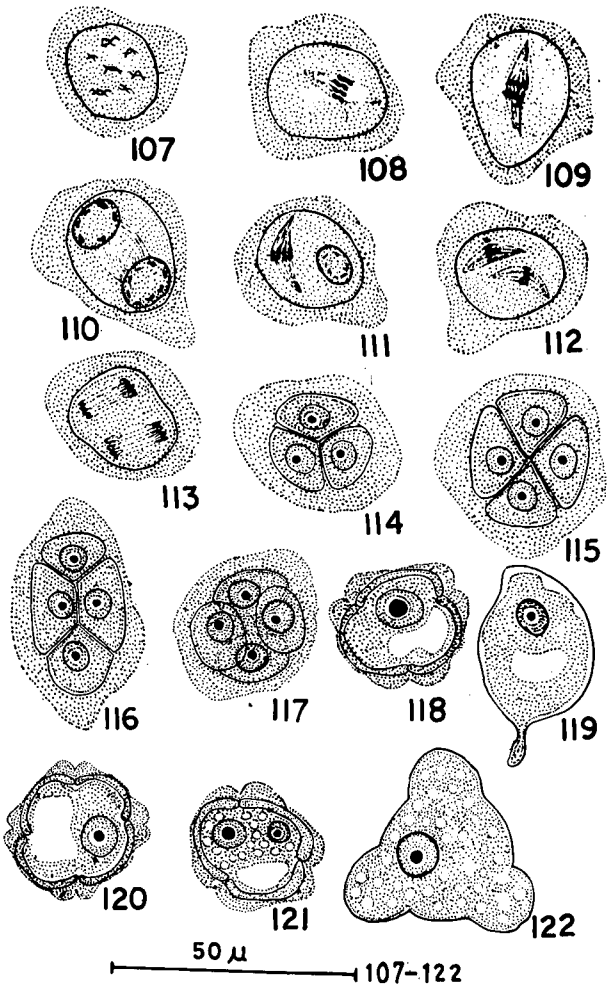
97
98
99
100
101
102
103
104
105
106
50 μ
92–106

EXPLANATION OF FIGURES

Figs. 107-122. Solanum cornutum. Microsporogenesis and male gametophyte. Figs. 107-110. Microspore mother cells showing diakinesis, metaphase I, anaphase I and telophase I of meiosis respectively. Fig. 111. Microspore mother cell showing non synchronous division. Figs. 112, 113. The microspore mother cell showing metaphase II and anaphase II of meiosis repectively. Figs. 114-117. Tetrahedral, isobilateral, rhomboidal and decussate microspore tetrads respectively. Fig. 118. Uninucleate pollen grain with vacuolated cytoplasm. Fig. 119. Uninucleate pollen grain showing in situ germination. Fig. 120. Tetracolporate pollen grain ith large vacuole. Fig. 121. 2-nucleate pollen grain. Fig. 122. Uninucleate pollen grain showing polysiphonous condition.


107
108
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114
115
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117
118
119
120
121
122
50 µ
107-122

MEGASPORANGIUM

The species of Solanum described in the present investigation show considerable differences in the form and structure of their ovules, and therefore, have been dealt with separately.

SOLANUM HISPIDUM AND S. RETROFLEXUM

The young placenta is composed of homogeneous cells. The places of initiation of ovules are marked early when the epidermis and two or three hypodermal layers become densely cytoplasmic and possess prominent nuclei. The hypodermal cells begin to divide in all directions and the epidermal cells covering these areas undergo anticlinal divisions. As a consequence small protuberances which appear on the surface of the young placenta constitute the primordia of the ovules. The ovules situated at the top of the placenta face towards the top of the ovary in Solanum hispidum, while the ovules in the middle region and at the bottom face downwards. Whereas in S. retroflexum the ovules face downwards.

The development of the ovules in S. hispidum and S. retroflexum essentially conforms to anatropous configuration and resembles with each other. Minor differences have been observed and described.

The nucellus is dome-shaped and covers the megaspore mother cell. It remains single layered throughout

in S. hispidum and S. retroflexum (Figs.123-125,129-131). The nucellus remains healthy upto the megaspore tetrad stage (Figs. 125, 131). Later, the nucellus degenerates completely, consequently the embryo sac at 2——nucle-ate stage becomes nacked (Figs. 126, 132). The primordium of the integument appears before the initiation of the meiotic divisions in the megaspore mother cell.The integument grows rapidly, reaches the level of the nucellus before the initiation of meiotic divisions (Figs. 124, 130). Meanwhile the ovule assumes hemianatropous configuration. The integument grows further, leaves the nucellus behind and forms a short and wide micropyle in S. hispidum (Fig. 125), while in S. retroflexum the micropyle is not formed at this stage (Fig. 131). The free-side of the integument consists of 5-6 layers of cells in the middle region. It is thin in the micropylar region (Fig. 125) while in S. retroflexum it is 4-5 layers of cells thick in the middle region (Fig. 131).The integument grows further and forms a long and narrow micropyle (Figs. 126, 132).

The ovule curves further and assumes almost anatropous configuration at 2-nucleate embryo sac stage. The ovule at four nucleate embryo sac stage exhibits anatropous configuration. The integument on the free side is 7-9 cells thick in the middle in S. hispidum and in S. retroflexum it is 6-7 cells thick. The integument on the funicular side is quite massive and is almost mearged

with the funicle (Figs. 127, 133). Thus the ovules in S. hispidum and S. retroflexum are anatropous, unitegmic and tenuinucellate.

The inner epidermis of the integument, which is in contact with the embryo sac differentiates as the integumentary tapetum or endothelium at 2-nucleate stage of the embryo sac. Its cells are densely cytoplasmic and possess prominent nuclei (Figs. 126-128, 132-134). The cells of the endothelium are radially elongated, surround the embryo sac and extend upto the tip of micropyle. The continuity of the endothelium is broaken at the chalazal side of the embryo sac (Figs. 126-128, 132-134). The endothelium persists upto the mature seed stage in S. hispidum while it degenerates at the globular stage of embryo in S. retroflexum.

A group of cells at the chalazal end differentiates as hypostase at the megaspore tetrad stage. It is situated towards the chalazal end below the embryo sac. The cells are compactly arranged, irregularly outlined and thick walled. They possess vacuolated cytoplasm. This tissue persists upto the mature embryo sac stage and degenerates after fertilization.

In several cases the young ovules have grown straight towards the ovary wall in S. hispidum. Such ovules could be called orthotropous.

SOLANUM FURCATUM AND S. DOUGLASII

The development of ovule in S. furcatum and S. douglasii essentially conforms to anatropous configuration and resembles with that in S. hispidum and S. retroflexum in the early developmental stages and differentiation of the nucellus. Following differences are worth recording.

The ovules at megaspore mother cell stage prior to the initiation of meiosis (Figs. 135, 136, 141, 142) are not so developed as in S. hispidum and S. retroflexum. The ovules at the megaspore tetrad stage in S. furcatum and S. douglasii assume almost anatropous configuration (Figs. 137, 143), whereas in S. hispidum and S. retroflexum the ovules at this stage are almost hemianatropous. The integument grows rapidly and forms a long and narrow micropylar canal (Figs. 137, 143). The ovules curve further and assume anatropous configuration (Figs. 138-140, 144-146). The integument on the free side in the middle region is 5-7 celled and 8-9 celled thick in S. furcatum and S. douglasii respectively (Figs. 140, 146), while on the funicular side it is quite massive and mearged with the funicle (Figs. 140, 146).

The inner epidermis of the integument differentiates as endothelium at megaspore tetrad stage in S. furcatum and S. douglasii, while in S. hispidum and S. retroflexum the endothelium differentiates at 2-nucleate stage of embryo sac. The endothelium persists upto post octant stage of embryo in S. furcatum and upto mature seed stage in S. douglasii.

The hypostase differentiates at the chalazal end of the ovule at megaspore tetrad stage (Figs.137-140, 143-146). It is irregular in outline and composed of thick walled cells, which possess vacuolated cytoplasm.

SOLANUM CORNUTUM

The development of ovule in S. cornutum conforms to the anatropous configuration. The early developmental stages of the ovule resemble the other described species of the genus (Figs. 147, 148).

The ovules at the megaspore tetrad stage do not show even complete hemianatropous structure. The integument at the free side is 4-5 layered thick. The nucellus remains healthy upto megaspore tetrad stage (Fig. 149). At the 2-nucleate stage the ovule curves and becomes almost hemianatropous (Fig. 150). The embryo sac enlarges considerably and the nucellus is completely absorbed at the 2-nucleate embryo sac stage. At the 4-nucleate stage of embryo sac the ovule curves further. The integument becomes 8-9 celled thick at the free side (Fig. 151). At the mature embryo sac stage the ovule becomes completely anatropous. The integument at this stage becomes 9-10 celled thick (Fig. 152).

The inner epidermis of the integument differentiates as endothelium at 2-nucleate stage of embryo sac. Its cells are densely cytoplasmic and possess prominent nuclei (Figs. 150-152). The cells of the endo-

thelium are radially elongated, surround the embryo sac except at the chalazal end, extend upto the tip of the micropyle.

The hypostase differentiates at the 2-nucleate stage of embryo sac in *C. cornutum* (Fig. 150). It is thick walled with vacuolated cytoplasm and irregularly shaped as in other species described here.

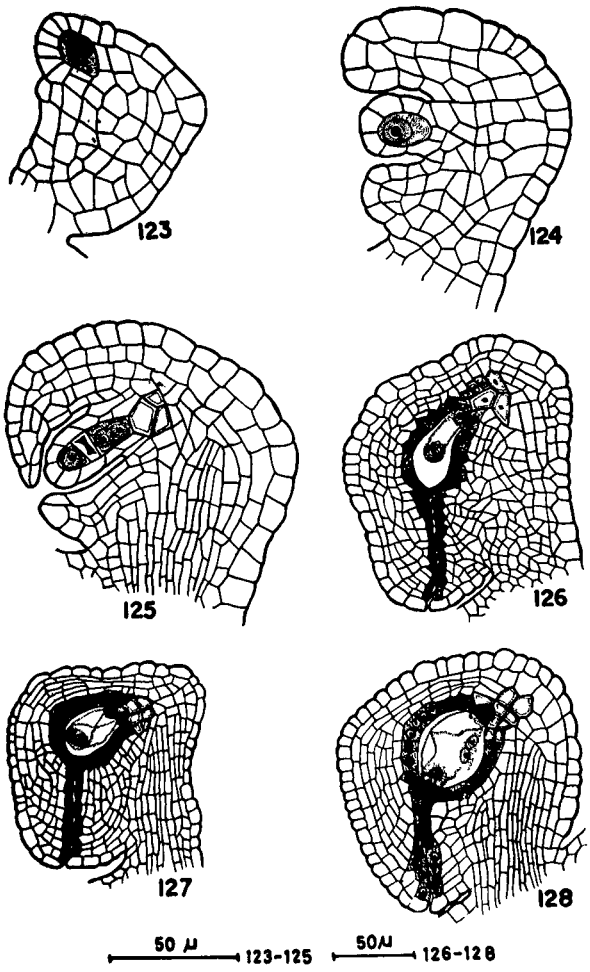
MEGASPORANGIUM

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Megasporangium	Anatropous unitegmic tenuinucellate	Anatropous unitegmic tenuinucellate	Anatropous unitegmic tenuinucellate	Anatropous unitegmic tenuinucellate	Anatropous unitegmic tenuinucellate
Nucellus degenerates	2-nucleate embryo sac	Megaspore tetrad	2-nucleate embryo sac	Megaspore tetrad	2-nucleate embryo sac
Endothelium differentiates	2-nucleate embryo sac	Megaspore tetrad	2-nucleate embryo sac	Megaspore tetrad	2-nucleate embryo sac
Hypostase develops	Megaspore tetrad	Megaspore tetrad	Megaspore tetrad	Megaspore tetrad	2-nucleate embryo sac
Ovule at megaspore tetrad	Hemianatropous	Almost anatropous	Hemianatropous	Almost anatropous	Hemianatropous
Ovule at 2-nucleate embryo sac	Almost anatropous	Anatropous	Almost anatropous	Anatropous	Almost Hemianatropous
Ovule at 4-nucleate embryo sac	Anatropous	Anatropous	Anatropous	Anatropous	Almost anatropous
Ovule at mature embryo sac	Anatropous	Anatropous	Anatropous	Anatropous	Anatropous
Integument comprises at mature embryo sac	7-9 cell layers	5-7 cell layers	6-7 cell layers	8-9 cell layers	9-10 cell layers

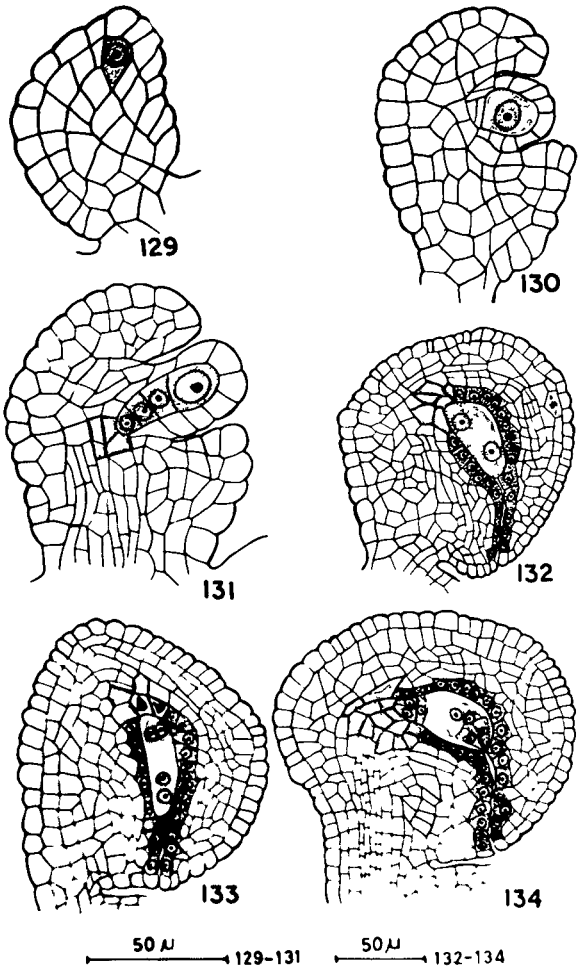
EXPLANATION OF FIGURES

Figs. 123-128. *Solanum hispidum*. Development of megasporangium. Fig. 123. L.s. young ovule showing archesporial cell. Fig. 124. L.s. ovule with megaspore mother cell. Fig. 125. L.s. ovule with megaspore tetrad. Figs. 126, 127. L.s. ovules with 2 and 4-nucleate embryo sacs respectively. Fig. 128. L.s. mature anatropous ovule showing mature embryo sac surrounded by endothelium. Hypostase is also seen.


123
124
125
126
127
128
50 μ
123-125
50μ
126-128

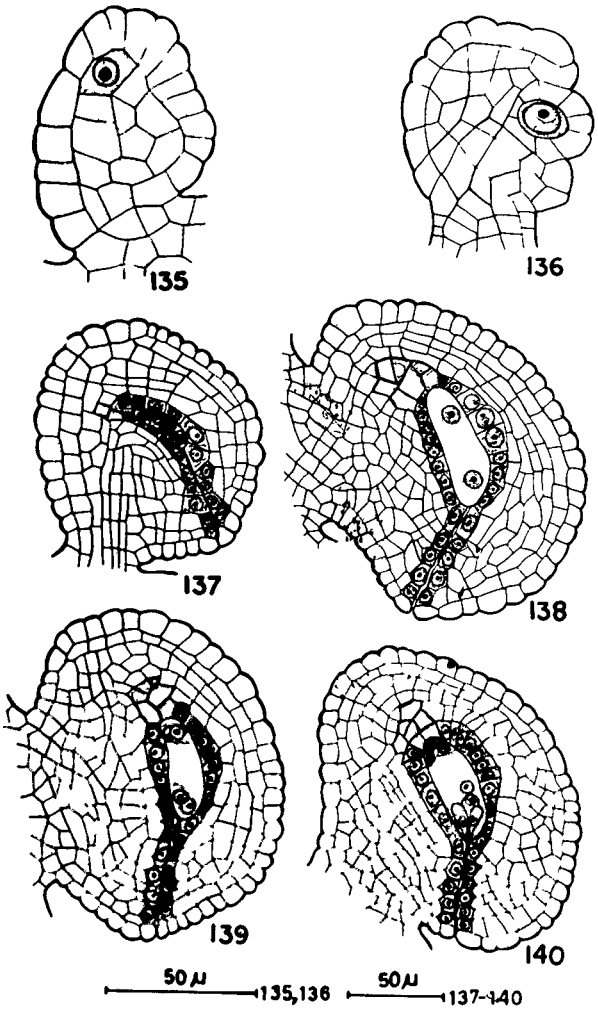
EXPLANATION OF FIGURES

Figs. 129-134. Solanum retroflexum. Development of megasporangium. Fig. 129. L.s. of young ovule showing female archesporial cell. Fig. 130. L.s. of ovule showing megaspore mother cell. Fig. 131. L.s. of ovule showing megaspore tetrad. Figs. 132, 133. L.s. of ovules showing 2- and 4-nucleate embryo sacs respectively. Fig. 134. L.s. anatropous unitegmic ovule showing mature embryo sac, endothelium and micropylar canal.


129
130
131
132
133
134
50 μ
129-131
50 μ
132-134

EXPLANATION OF FIGURES

Figs. 135-140. Solanum furcatum. Development of megasporangium. Fig. 135. L.s. ovule showing female archesporial cell. Fig. 136. L.s. of ovule at megaspore mother cell stage. Fig. 137. L.s. of ovule at megaspore tetrad stage. Endothelium and hypostase have differentiated. Figs. 138, 139. L.s. ovules showing 2 and 4-nucleate embryo sacs respectively. Fig. 140. L.s. anatropous ovule showing mature embryo sac, micropylar canal and hypostase.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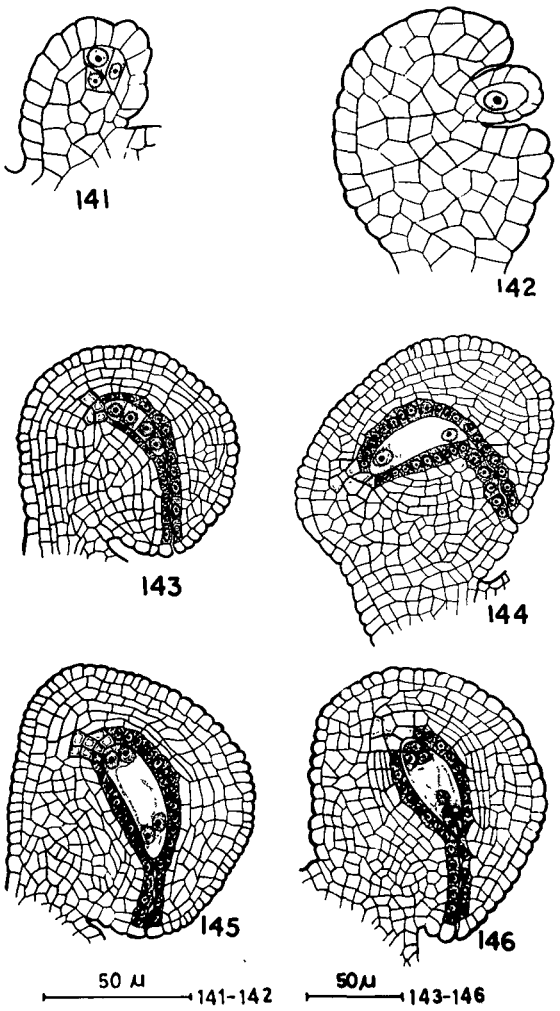
EXPLANATION OF FIGURES

Figs. 141-146. Solanum douglasii. Development of megasporangium. Fig. 141. L.s. of ovule, nucellus covering the female archesporial cells. Fig. 142. L.s. ovule at megaspore mother cell stage. Fig. 143. L.s. of ovule at megaspore tetrad stage, endothelium has also differentiated. Figs. 144, 145. L.s. of ovules at 2 and 4-nucleate embryo sacs respectively. Fig.146.L.S. anatropous ovule showing mature embryo sac, endothelium, micropylar canal and hypostase.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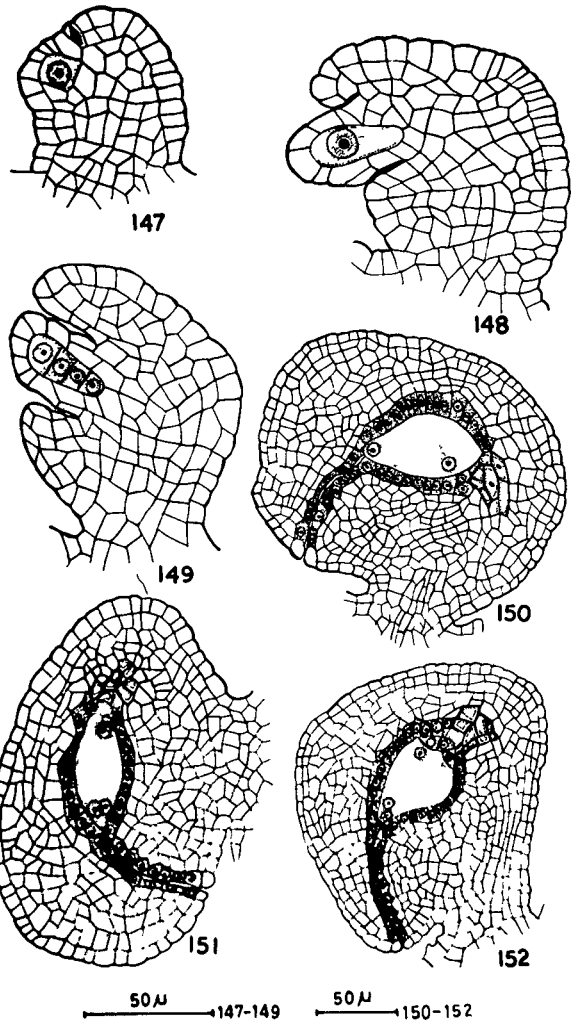
EXPLANATION OF FIGURES

Figs. 147-152. *Solanum cornutum*. Development of megasporangium. Fig. 147. L.s. of ovule showing female archesporial cell. Fig. 148. L.s. ovule showing megaspore mother cell. Fig. 149. L.s. ovule showing megaspore tetrad. Fig. 150. L.s. of almost hemianatropous ovule.showing 2-nucleate embryo sac. Fig. 151. L.s. of almost anatropous ovule at 4-nucleate embryo sac stage. Fig. 152. L.s. mature anatropous unitegmic ovule showing mature embryo sac, endothelium, a long micropylar canal and hypostase.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MEGASPOROGENESIS

The female archesporium differentiates at an early stage of ovule development. It is hypodermal in origin, situated at the apex of the ovule primordium and attains significant size. It is densely cytoplamic and possesses a prominent nucleus (Figs. 153, 180,208,225, 243). The archesporial cells are somewhat narrow and elongated in Solanum hispidum, S. retroflexum and S. douglasii (Figs. 153, 208, 225), while almost isodiametric in S. furcatum and S. cornutum (Figs. 180,243). The archesporium is generally single celled (Figs.153, 180, 208, 225, 243). Occasionally it may be 2-celledin S. hispidum, S. furcatum, S. retroflexum and S. cornutum (Figs. 154, 181, 209, 210, 244), 3-celled in S. douglasii and S. cornutum (Figs. 226, 245) and upto 5-celled in S. hispidum (Fig. 155). In a multicellular archesporium the cells may be situated side by side (Figs. 181, 209, 244) or one above the other(Figs.154, 210, 245).

The archesporial cells do not cut off parietal cells and directly differentiates as megaspore mother cells. The megaspore mother cells undergo meiosis producing megaspore tetrads (Figs. 156-165, 182-194, 211-213, 227-229, 246-254). After the first meiotic divisions two dyad cells are formed (Figs. 156-158, 182-186, 211, 212, 227, 228, 246-248). In one case,a megaspore mother cell at metaphase I and two dyad cells

are situated side by side in S. furcatum (Fig.185). The meiotic divisions in the dyad cells may not be synchronous in S. hispidum, S. furcatum and S. cornutum (Figs. 159-161, 163, 164, 187-190, 249-251), but sometimes the divisions are synchronous in S. hispidum and S.furcatum (Figs. 162, 191). The division in the micropylar dyad cell generally precedes that in chalazal one in S. hispidum and S. cornutum (Figs. 159-161, 249), but sometimes the divisions in the micropylar dyad cell may lag behind in S. hispidum (Fig. 163), S. furcatum (Figs.188-190) and S.cornutum (Fig. 251).

The megaspore tetrads are generally linear in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum (Figs. 162-165, 189-192, 213, 229,249-252). Sometimes the megaspore tetrads may be T-shaped in S. furcatum (Figs. 193, 194). Inverted T-shaped megaspore tetrads may rarely develop in S. hispidum and S. cornutum (Figs. 168, 253). In an exceptional case in S. retroflexum an isobilateral megaspore tetrad has been observed (Fig. 216). In another case the megaspore tetrad is almost rhomboidal in S. cornutum (Fig. 254). In one case polyspory has been observed in S. hispidum (Fig. 169). There are five megaspores, two megaspores are situated towards micropylar and chalazal sides each and the fifth megaspore is situated in between them (Fig. 169).

It is interesting to record that in a large number of cases in S. hispidum it has been observed that some

cells of the integument or nucellus enlarge considerably and behave as accessory archesporial cells. In one case in S. hispidum there is a linear megaspore tetrad and an archesporial cell also is seen near it (Fig. 166). In another similar case two archesporial cells are situated below the linear megaspore tetrad (Fig. 167). Accessory archesporial cells have also been observed in S. douglasii (Figs. 230-232). In one case in S. douglasii an archesporial cell is situated below the megaspore tetrad whose two micropylar megaspores have degenerated while the chalazal ones are healthy (Fig. 230). In another case two archesporial cells, one of them is dividing, are situated towards the funicular side of the ovule near 2-nucleate embryo sac (Fig. 231).

Usually the chalazal megaspore is functioning and the remaining three degenerate (Figs. 170, 195, 214,233, 255). Considerable variations in the number of healthy megaspores in a tetrad have been observed in S.hispidum, S. furcatum, S. retroflexum and S. douglasii. Occasionally two megaspores situated at the chalazal side may be healthy in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum (Figs. 171, 196, 215, 216, 234, 256), while the two micropylar ones degenerate.Sometimes the two middle megaspores of a linear tetrad may degenerate in S. furcatum and S. douglasii (Figs. 197, 235), while the micropylar and chalazal ones are healthy. Occasionally three chalazal megaspores may be healthy-while the micropylar one degenerates in S. hispidum, S.

furcatum and S. douglasii (Figs. 172, 199, 236).Sometimes the second megaspore from the micropylar side may degenerate and the remaining three show healthy appearance in S. hispidum and S. furcatum (Figs. 173, 200). Rarely the third megaspore from the micropylar side may degenerate and the remaining three are healthy in S. hispidum, S. furcatum and S. douglasii (Figs. 174, 198, 237). In one case in S. furcatum all the four megaspores in a linear tetrad are healthy (Fig. 201). The chalazal megaspore has divided to produce 2-nucleate embryo sac (Fig. 201). In an isobilateral tetrad both the micropylar megaspores may degenerate while the two chalazal megaspores may remain healthy in S. retroflexum (Fig. 216).

FEMALE GAMETOPHYTE

The development of female gametophyte in the species described here conforms to the Polygonum type. The functional megaspore attains a significant size and comes to possess terminal vacuoles (Figs. 238, 257), then its centrally situated nucleus divides to give rise to two nucleate embryo sac in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum (Figs. 175, 202, 217, 239, 258). The two nuclei remain close together for a time but soon the embryo sac begins to enlarge, the nuclei move apart to the opposite poles of the sac and a large central vacuole is formed (Figs. 175, 202, 217, 239, 258). The second division in the nuclei of two nucleate embryo sac may be simultaneous in S. hispidum, S. retroflexum and S. douglasii (Figs. 176, 217, 218, 240), whereas in S. furcatum and S. cornutum the second division may not be synchronous (Figs. 203, 259). The two nuclei at each pole divide and 4-nucleate embryo sac is formed (Figs. 176, 177, 203, 204, 218, 240, 241, 259). The third nuclear division in the embryo sac is synchronous in S. furcatum, S. retroflexum, S. douglasii and S. cornutum, while in S. hispidum (Fig. 178) the third division is not synchronous. The chalazal nuclei may divide earlier than the micropylar ones. Ultimately 8-nucleate embryo sac is formed. The four nuclei are arranged at the chalazal and four at the micropylar end of the embryo sac. The micropylar quartet gives rise to egg

apparatus, which is organized at the extreme apex of the sac. It consists of one egg cell and two synergids(Figs. 179, 205, 219, 242, 260). The synergids are situa-ted side by side and the egg extends below them. Fourth nucleus of the micropylar quartet behaves as micropylar polar nucleus. The three nuclei of the chalazal quartet give rise to well organized antipodal cells at the chalazal end of the embryo sac (Figs. 179, 205, 219, 242, 260). The antipodal cells have triangular arrangement. The two antipodal cells may be situated side by side and the third below them towards the chalazal side (Figs.179, 205, 219, 242, 260) or vice-versa (Figs. 220,221). Rarely the antipodals may be placed side by side in S. cornutum (Fig. 264). Fourth nucleus of the chalazal quartet behaves as chalazal polar nucleus. In S. hispidum both the polar nuclei are seen in the centre of the sac (Fig. 179), whereas in S. retroflexum the polar nuclei are seen at the chalazal side (Fig. 219). In S. furcatum and and S. douglasii the polar nuclei fuse forming secondary nucleus before the entry of the pollen tube into the sac. The secondary nucleus is seen in the centre of the sac (Figs. 205, 242). Thus the development of the female gametophyte in all the species described here conforms to the Polygonum type.

Variations in the number and arrangement of nuclei in female gametophyte have been observed. In S. furcatum in one case two big free nuclei with multinucleolate condition are seen at the micropylar end (Fig. 206). It

appears that the two nuclei after first mitotic division migrated towards the micropylar side where they divided and the resultant nuclei fused forming two large multinucleolate nuclei. In another case five free nuclei are situated towards the micropylar side in S.furcatum (Fig. 207). In a similar case in S. cornutum three free nuclei have been observed at the chalazal end (Fig. 261). Probably the nuclei after first mitotic division either did not migrate to the opposite poles or the nuclei moved towards micropylar or chalazal side. It also appears that one of the nuclei of 4-nucleate embryo sac had divided producing five nuclei aggregated at the micropylar side. In an exceptional 8-nucleate embryo sac the egg is situated at the base of the micropyle while the synergids are organized below the egg (Fig. 221). In one case in a 5-nucleate embryo sac the egg apparatus is composed of only egg, which is situated towards the micropylar side. There are three antipodal cells and a polar nucleus is seen near the antipodals (Fig. 222). Occurrence of organized embryo sac with less than eight nuclei may be interpretted due to suppression of second and third mitotic divisions in the nucleus situated at the micropylar side, while the chalazal nucleus at the chalazal pole behaves normally.

In S. retroflexum in a 4-nucleate embryo sac three antipodal cells are arranged at the chalazal end and one free nucleus is seen at the micropylar side (Fig. 223). In a similar case in S. cornutum the free nucleus is situated near the antipodal cells (Fig. 262). Still in

another case in a 5-nucleate embryo sac three antipodal cells are arranged at the chalazal end and two free nuclei are also seen near the antipodals (Fig. 263). In an exceptional 5-nucleate embryo sac in S. cornutum the three antipodal cells are placed side by side at the chalazal end, one free nucleus is seen at the chalazal end and the other at the micropylar end (Fig.264).Variations in the number of nuclei or cells on either pole in the embryo sac may be due to the suppression of mitotic divisions.

Rarely twin embryo sacs have also been observed. In one case two embryo sacs, one at 6-nucleate stage and the other at 8-nucleate stage are placed side by side in S. retroflexum (Fig. 224).

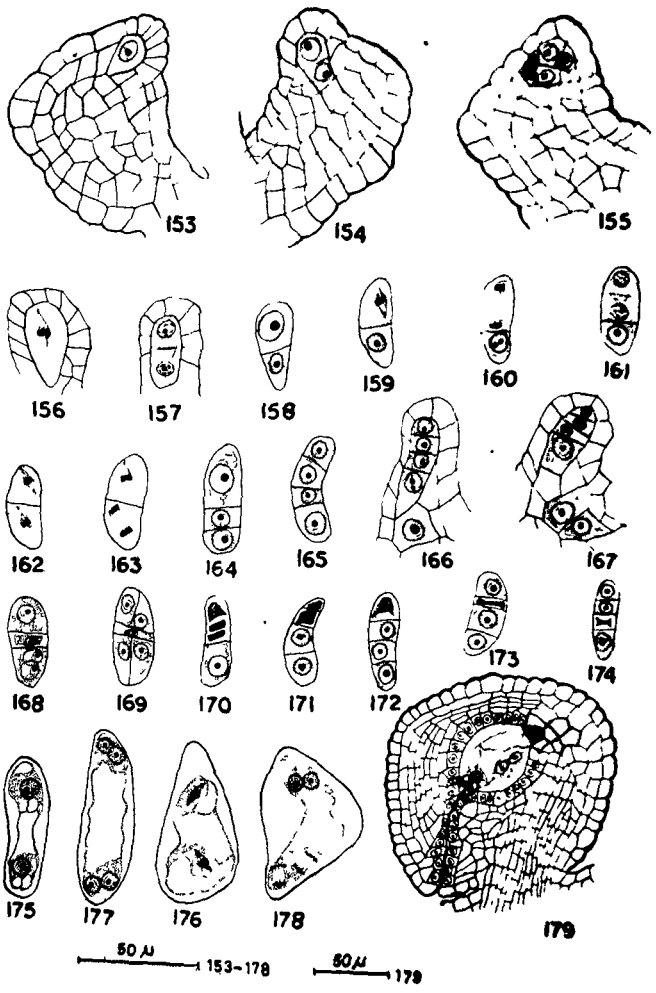
MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Female archesporium	Single-celled Occasionally upto 5-celled	Single-celled Occasionally 2-celled	Single-celled Occasionally 2-celled	Single-celled Occasionally upto 3-celled	Single-celled Occasionally upto 3-celled
Accessory archesporium	Present	Absent	Absent	Present	Absent
Megaspore tetrads	Linear Rarely Inverted T-shaped and Polysporad	Linear Sometimes T-shaped	Linear Rarely isobilateral	Linear	Linear Rarely Inverted T-shaped and rhomboidal
Functional Megaspore	Chalazal	Chalazal	Chalazal	Chalazal	Chalazal
Female gametophyte	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type	Monosporic 8-nucleate Polygonum type
Fusion of polar nuclei	Do not fuse	Fuse forming secondary nucleus	Fuse forming secondary nucleus	Fuse forming secondary nucleus	Do not fuse
Twin sacs	Absent	Present	Absent	Absent	Absent

EXPLANATION OF FIGURES

Figs. 153-179. Solanum hispidum. Megasporogenesis and female gametophyte. Figs. 153-155. L.s.ov-ules showing 1, 2 and multicellular archesporium respectively. Figs. 156, 157. L.s. part of ovules showing megaspore mother cells at metaphase I and telophase I respec—tively. Fig. 158. Dyad. Figs. 159, 160, 161.The micropylar dyad cell undergoing division. Figs. 162,163. Dividing dyad cells. Fig. 164. Triad. Fig. 165. Linear megaspore tetrad. Figs. 166, 167. One and two accessoryarchesporial cells situated below linear megaspore tetrad rospectively. Fig. 160. Inverted T-shaped megaspore tetrad. Fig. 169. Polyspory.Fig.170. Chalazal megaspore is functioning while remaining have degenerated. Fig. 171. Two micropylar megaspores have degenerated while the two chalazal ones are healthy. Fig. 172. The micropylar megaspore of a linear megaspore tetrad has degenerated while remaining three are healthy. Fig. 173. Second megaspore from the micropylar side has degenerated while the other three are healthy. Fig. 174. Third megaspore from the micropylar side has degenerated while remaining three are healthy. Fig. 175. 2-nucleate embryo sac.Fig.176. The nuclei of 2-nucleate embryo sac dividing.Fig.177. 4-nucleate embryo sac. Fig. 178. 4-nucleate embryo sac, the nuclei at the chalazal end are dividing.Fig. 179. L.s. mature anatropous unitegmic ovule showing mature embryo sac surrounded by the endothelium, long micropylar canal and hypostase.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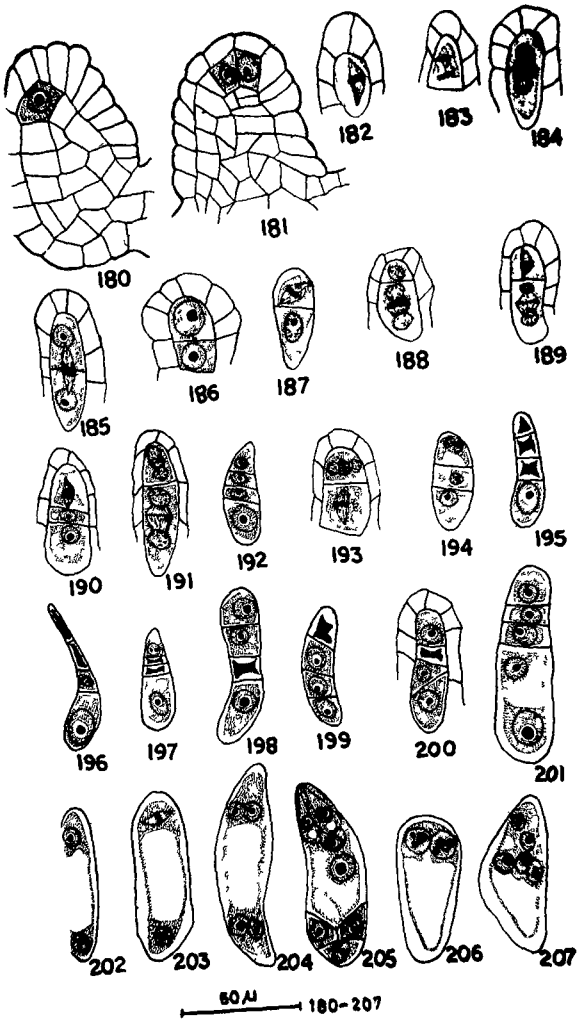
EXPLANATION OF FIGURES

Figs. 180-207. Solanum furcatum. Megasporogenesis and female gametophyte. Figs. 180, 181. L.s. of ovules showing 1 and 2 archesporial cells respectively. Figs. 182-184. L.s. part of ovules showing dividing megaspore mother cells. Fig. 185. Dyad and megaspore mother cell at metaphase 1 stage. Fig. 186. Dyad. Fig. 187. Micropylar dyad cell undergoing division. Fig. 188. Chalazal dyad cell undergoing division. Fig.189. Dyad cells showing second meiotic divisions. Fig.190. The division in chalazal dyad cell is complete while the micropylar one is dividing. Fig. 191. Dividing dyad cells. Fig. 192. Linear megaspore tetrad. Figs. 193, 194. T-shaped megaspore tetrads. Fig. 195. Chalazal megaspore is functioning while the three micropylar ones have degenerated. Fig. 196. Two micropylar megaspores have degenerated while the two chalazal ones are healthy. Fig. 197. The micropylar and chalazal megaspores are healthy while the middle two have degenerated. Fig. 198. Second megaspore from the chalazal side has degenerated while the remaining three are healthy. Fig. 199. Micropylar megaspore has degenerated while the remaining three are healthy. Fig. 200. Second megaspore from the micropylar side has degenerated while remaining three are healthy. Fig. 201. Linear megaspore tetrad; the chalazal megaspore has divided to produce 2-nucleate embryo sac.Fig.202. 2-nucleate embryo sac. Fig. 203. 2-nucleate embryo sac, the nucleus at the micropylar end is dividing.Fig. 204. 4-nucleate embryo sac. Fig. 205. Mature embryo sac. Fig. 206. 2-nucleate embryo sac, the nuclei are situated at the micropylar end. Fig. 207. 5-nucleate embryo sac, all the nuclei are aggregated at the micropylar end of the sac.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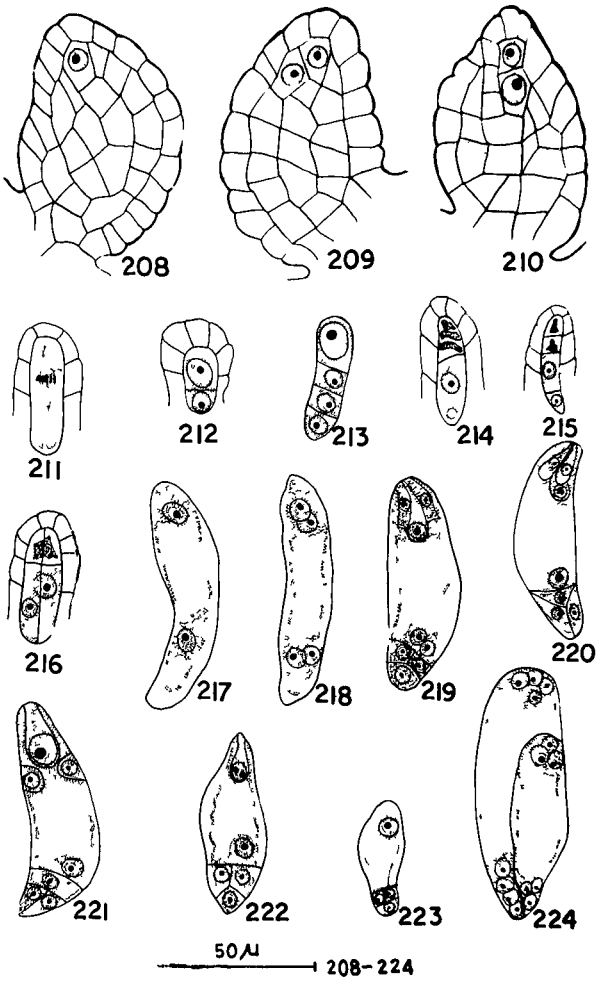
EXPLANATION OF FIGURES

Figs. 208-224. Solanum retroflexum. Megasporogenesis and female gametophyte. Fig. 208. L.s. young ovule showing female archesporial cell. Figs. 209, 210. L.s. of ovules showing 2-celled archesporium. Fig. 211. Megaspore mother cell at metaphase I stage. Fig. 212. Dyad. Fig. 213. Linear megaspore tetrad. Fig. 214. Three micropylar degenerated and chalazal healthy megaspores. Fig. 215. Two micropylar megaspores degenerated while chalazal ones are healthy. Fig. 216. Isobilateral megaspore tetrad. The two micropylar megaspores have degenerated. Fig. 217. 2-nucleate embryo sac. Fig. 218. 4-nucleate embryo sac. Fig. 219. Mature embryo sac showing 3-celled egg apparatus, two polar nuclei at the chalazal end and 3 antipodal cells. Fig. 220. Mature embryo sac showing 3-celled egg apparatus, secondary nucleus situated at the chalazal end and three antipodal cells. Fig. 221. Mature embryo sac. The egg is situated at the extreme micropylar end while the synergids are situated below it. Fig. 222. 5-nucleate embryo sac showing three antipodal cells, one egg and one free nucleus in the centre of the sac. Fig. 223. 4-nucleate embryo sac showing one free nucleus towards the micropylar side and three antipodal cells at the chalazal end. Fig. 224. Twin embryo sacs placed side by side; one sac is 8-nucleate and the other at 6-nucleate stage.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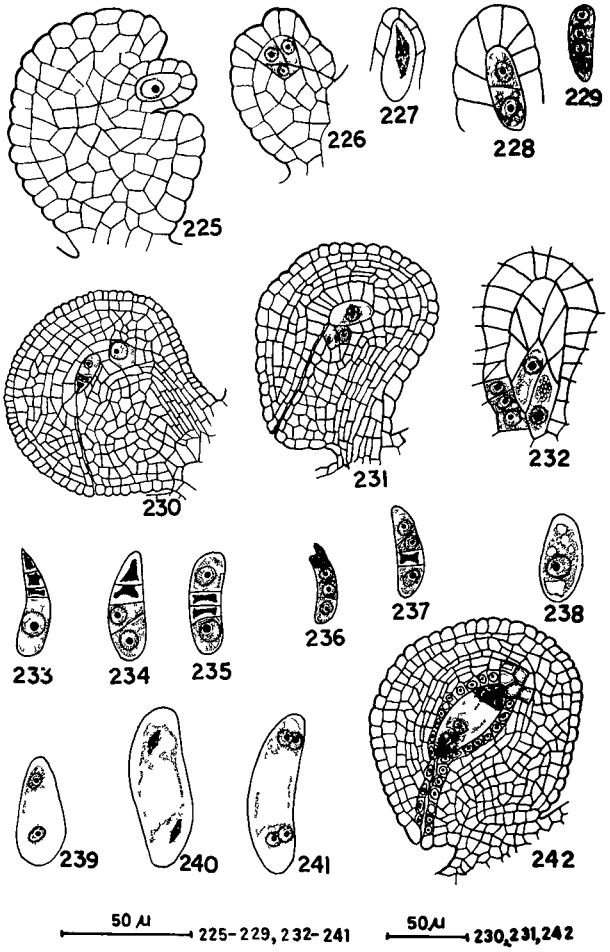
EXPLANATION OF FIGURES

Figs. 225-242. *Solanum douglasii*. Megasporogenesis and female gametophyte. Figs. 225, 226. L.s. young ovules showing 1 and 3 archesporial cells respectively. Fig. 227. Megaspore mother cell at metaphase I stage. Fig. 228. Dyad. Fig. 229. Linear megaspore tetrad. Fig. 230. L.s. ovule showing megaspore tetrad and an accessory archesporial cell. Fig. 231. L.s. ovule showing 2-nucleate embryo sac and two accessory archesporial cells, one of them is dividing. Fig. 232. L.s. part of ovule showing accessory archesporial cells. Fig. 233. Chalazal functional and three micropylar degenerated megaspores. Fig. 234. Two chalazal healthy megaspores and two micropylar ones degenerated. Fig. 235. Micro-pylar and chalazal megaspores are healthy while the two middle megaspores have degenerated. Fig. 236. The micropylar megaspore of a linear megaspore tetrad has degenerated while remaining three are healthy. Fig. 237. Second megaspore from the chalazal side degenerated while the remaining three are healthy. Fig. 238. Functional megaspore. Fig. 239. 2-nucleate embryo sac. Fig. 240. Both the nuclei of 2-nucleate embryo sac are dividing. Fig. 241. 4-nucleate embryo sac. Fig. 242. L. s. mature anatropous ovule showing mature embryo sac, endothelium and hypostase.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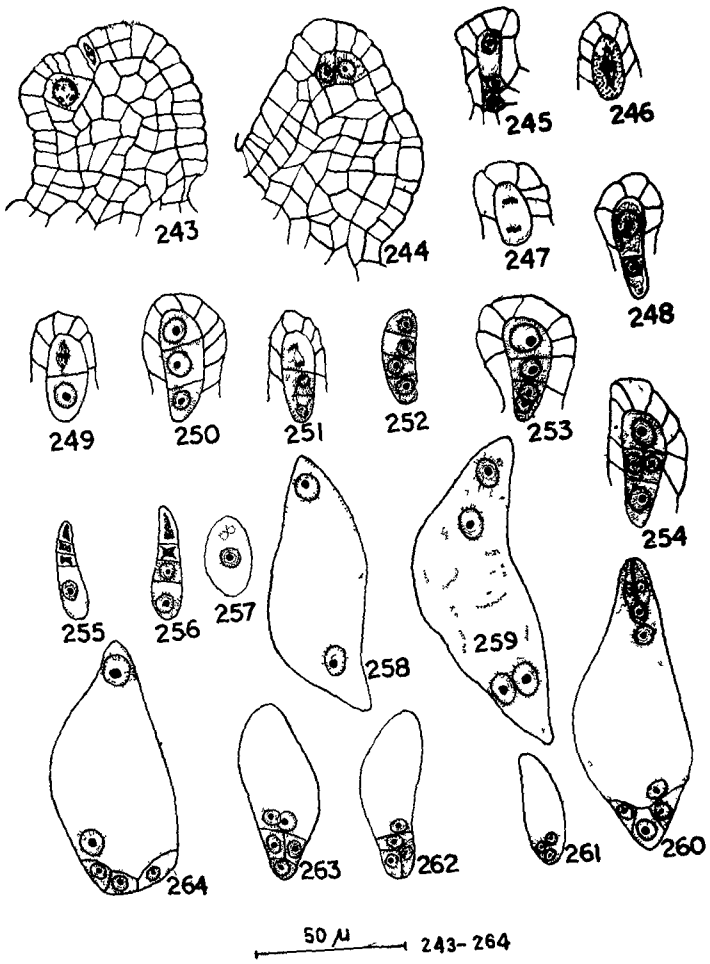
EXPLANATION OF FIGURES

Figs. 243-264. *Solanum cornutum*. Megasporogenesis and female gametophyte. Figs. 243, 244. L.s. ovules showing 1 and 2 archesporial cells respectively. Fig. 245. L.s. part of young ovule showing three archesporial cells placed one above the other. Figs. 246, 247. Megaspore mother cells undergoing division. Fig.248. Dyad. Fig. 249. The micropylar dyad cell is dividing. Fig. 250. Triad. Fig. 251. Dyad cells showing second meiotic divisions. Fig. 252. Linear megaspore tetrad. Fig. 253. Inverted T-shaped megaspore tetrad. Fig.254.Rhomboidal megaspore tetrad. Fig. 255. Chalazal functional megaspore, the three micropylar ones have degenerated. Fig. 256. The two chalazal megaspores are healthy while the micropylar ones have degenerated. Fig. 257. Functional megaspore. Fig. 258. 2-nucleate embryo sac. Fig. 259. 4-nucleate embryo sac. Fig. 260. Mature embryo sac. Fig. 261. 3-nucleate embryo sac. All the three nuclei are situated at the chalazal end.Fig.262. 4-nucleate embryo sac showing 3 antipodal cells and one free nucleus near the antipodals. Fig.263.5-nucleate embryo sac showing 3 antipodal cells and two nuclei are seen near them. Fig. 264. 5-nucleate embryo sac showing 3 antipodal cells lying side by side and two free nuclei, one towards the chalazal side and the other towards the micropylar end.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POLLINATION AND COURSE OF POLLEN TUBE

The stigma is capitate in Solanum furcatum, S. retroflexum and S. douglasii (Fig. 265). In S. hispidum and S. cornutum the stigma is bilobed and both the lobes are separate upto a considerable length of style (Figs. 266, 268, 269). The stigma is papillate. The stigmatic papillae in S. furcatum, S. retroflexum, S. douglasii (Fig.265) and S. hispidum (Fig. 266) are almost tubular while in S.cornutum (Fig. 268)the tips are rounded. The style is solid devoid of any special transmitting tissue for the pollen tube. However, the style may be hollow upto a limited extent in S. hispidum and S. cornutum (Figs. 266,268,269). In S. hispidum the stigma becomes curved after pollination (Fig. 267).

The pollination is anemophilous. The pollen grains are seen entangled between the stigmatic papillae where they germinate. The pollen tubes creep between the stigmatic papillae and enter the stylar tissue. They grow down through the intercellular spaces of the stylar cells without damaging them, reach the base of the style and enters the ovarian cavity. Thus a bundle of pollen tubes reaches the top of the placenta and covers the ovules, situated at the top of the ovarian cavity. Later the pollen tubes move away in all directions on the placental surface and finally enter the ovule through the micropyle.

POLLINATION

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Stigma	Bilobed	Capitate	Capitate	Capitate	Bilobed
Stigmatic papillae	Tubular	Tubular	Tubular	Tubular	Rounded
Style	Hollow upto limited extent	Solid	Solid	Solid	Hollow upto limited extent
Pollination	Anemophilous	Anemophilous	Anemophilous	Anemophilous	Anemophilous

FERTILIZATION

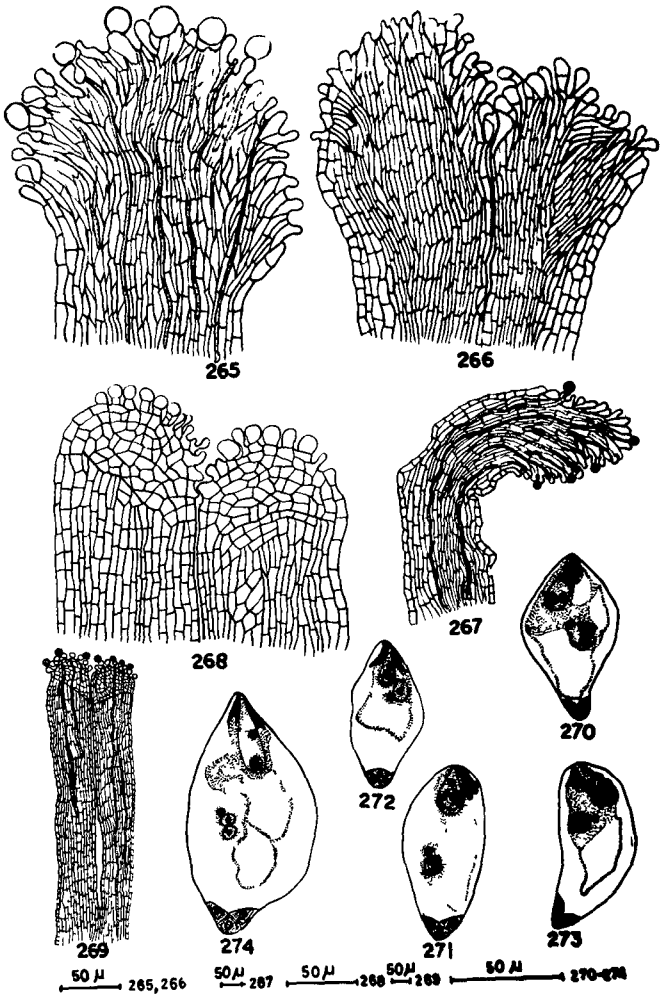
At the time of pollination the embryo sacs in the ovules, situated at the top of the placenta, are mature and ready to receive the pollen tubes. Prior to its entry into the embryo sac the pollen tube is a delicate cylindrical structure, but becomes irregular in shape and quite conspicuous inside the sac. The pollen tube enters the embryo sac near one of the synergids. May be, some chemotactic substance is secreted by the cells of egg apparatus or the wall of the sac in that region is weak. During the entry of the pollen tube into the sac generally one synergid is destroyed. Later the other synergid also is destroyed during the act of fertilization.

One of the male gametes fuses with the egg nucleus and the second one is seen in the vicinity of secondary nucleus in *Solanum furcatum*, *S. retroflexum* and *S. douglasii* (Figs. 271-273), while in *S. hispidum* and *S. cornutum* the second male gamete is observed near the polar nuclei (Figs. 270, 274). Thus as a result of fusion of second male gamete with the secondary nucleus or polar nuclei primary endosperm nucleus is formed.

The remains of the pollen tube may persist inside the embryo sac till 2-3 celled endosperm stage.

EXPLANATION OF FIGURES

Figs. 265-269. Pollination. Figs. 270-274. Solanum hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum respectively. Fertilization. Fig. 265. L.s. stigma of S. furcatum showing pollination. Pollen tubes are seen in the stylar tissue. Fig. 266. L.s. bifid stigma of S. hispidum. Fig. 267. L.s. style and curved stigma of S. hispidum showing germinated pollen grains on the stigma and pollen tubes in the stylar tissue. Fig. 268. L.s. bifurcated stigma of S. cornutum showing papillae. Fig. 269. L.s. style and stigma showing germinated pollen grains on the stigma of S.cornutum and pollen tubes in the stylar tissue. Figs. 270-274. Embryo sacs showing double fertilization.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ENDOSPERM

The development of endosperm in Solanum hispidum, S. furcatum, S. retroflexum, S. douglasii and S.cornutum is ab initio Cellular. However, variations in the plane of divisions in the early stages of endosperm development have been observed in different species described here. Therefore for the sake of clarity the development of endosperm in different species has been described separately.

The development of endosperm starts more or less immediately after fertilization while the division of the zygote is delayed unless sufficient amount of endosperm is formed.

SOLANUM HISPIDUM

The development of endosperm in Solanum hispidum is ab initio Cellular. The primary endosperm nucleus divides transversely producing primary micropylar and primary chalazal endosperm chambers (Figs. 275, 276). The division in both the chambers is vertical producing 4-celled endosperm (Figs. 277, 278). Further, the development of endosperm could not be observed successfully because of abnormal behaviour of the endothelium. The cells of the endothelium proliferate and produce adventive embryos (Fig. 277), which fill the cavity of the embryo sac.Thus the development of the endosperm could not be followed successfully. However, the divisions in the later stages

of endosperm development become irregular and the endosperm becomes multicellular (Fig. 279).

SOLANUM FURCATUM

The development of endosperm in Solanum furcatum is ab initio Cellular. The first division of the primary endosperm nucleus is transverse dividing the sac into primary micropylar and primary chalazal endosperm chambers (Figs. 280-281). The division in either chamber may precede the other (Figs. 282, 283). The division in both the endosperm chambers is longitudinal. Thus four celled endosperm is produced (Fig. 284). The two juxtaposed cells of primary micropylar and primary chalazal endosperm chambers divide longitudinally producing 8-celled endosperm (Figs. 285, 286). Later, the divisions become irregular.

Variations in the plane and sequence of cell divi - sions during the early stages of endosperm development have also been observed. In one case one of the juxtaposed cells of primary micropylar endosperm chamber has divided longitudinally while the other transversely(Fig. 287). In a 6-celled endosperm one of the juxtaposed cells of the micropylar endosperm chamber has divided longitudinally while the primary chalazal endosperm chamber has divided transversely producing two cells, of which the chalazal cell has not yet divided while the upper one has divided longitudinally (Fig. 288). In another similar case the primary chalazal endosperm chamber has

divided transversely producing two cells, the chalazal one has divided transversely while the upper one longitudinally (Fig. 289). The two juxtaposed cells of micropylar endosperm chamber have divided transversely(Fig.289). Still in another case the primary chalazal endosperm chamber has divided transversely producing two superposed cells. The chalazal cell has divided longitudinally producing two juxtaposed cells, one of which has divided longitudinally while the other transversely. The two micropylar cells have divided longitudinally (Fig. 290). In a four celled endosperm it has been observed that the primary micropylar endosperm chamber has divided longitudinally while the primary chalazal endosperm chamber transversely forming four cells arranged in a T-shaped manner (Fig.291). Occasionally the primary micropylar and primary chalazal endosperm chambers divide transversely producing four linearly arranged cells (Figs. 292, 293). In a similar case five cells are arranged linearly (Fig. 294). Rarely the first division in the primary endosperm cell may be longitudinal producing two unequal cells of endosperm.The larger cell has divided transversely (Fig. 295).

SOLANUM ROTROFLEXUM

The development of endosperm is ab initio Cellular. The first division in the primary endosperm nucleus is transverse producing primary micropylar and primary chalazal endosperm chambers (Figs. 296, 297). The division in the primary micropylar endosperm chamber precedes that

in chalazal one (Figs. 298, 299). The division in both the endosperm chambers is longitudinal. Thus four celled endosperm is produced (Figs. 298-300). The division in the two juxtaposed cells of primary micropylar endosperm chamber is transverse while the division in the cells of the primary chalazal endosperm chamber is longitudinal (Figs. 301-304). Later, the divisions become irregular.

Variations in the plane of divisions in the early stages of endosperm development have been observed. In one case one of the two juxtaposed cells of primary micropylar endosperm chamber has divided transversely while the other longitudinally (Fig. 305). In another case it has been observed that the two juxtaposed cells of primary chalazal endosperm chamber have divided transversely (Fig. 306). Still in another case it appears that the two juxtaposed cells of chalazal endosperm chamber have divided transversely, while the micropylar cells have divided longitudinally (Fig. 307). Sometimes the division in the primary chalazal endosperm chamber is transverse, while the micropylar endosperm chamber has divided longitudinally, thus the four cells are arranged in a T-shaped manner (Fig. 308). In another similar case the second cell from the chalazal end has divided longitudinally (Fig. 309). In an exceptional case, the primary micropylar endosperm chamber has divided trans-

versely, while the chalazal one longitudinally (Fig . 310). In one case it has been observed that the primary endosperm nucleus has divided obliquely vertical producing two unequal endosperm cells, which have divided longitudinally. Further divisions in these cells have been irregular (Fig. 311).

SOLANUM DOUGLASII

The development of endosperm is ab initio Cellular. The first division in the primary endosperm cell is transverse, dividing the embryo sac into primary micropylar and primary chalazal endosperm chambers (Figs. 312, 313). The division in either chamber may precede the other (Figs. 314, 315). The division in both the primary endosperm chambers is longitudi-nal , thus four completely partitioned cells are produced (Fig. 316). Sometimes the division in the primary chalazal endosperm chamber is delayed considerably while four cells are formed in the micropylar chamber (Fig. 317). The two juxtaposed cells of micropylar and chalazal endosperm chambers divide transversely (Figs. 318, 319). Later the divisions in the cells of the endosperm are quite irregular forming multicellular endosperm (Fig. 326).

Variations in the plane and sequence of cell divisions have been observed during the early stages of endosperm development. In one case two juxtaposed cells of primary micropylar and primary chalazal endos-

perm chambers have divided longitudinally producing 6-celled endosperm (Fig. 320). In another case the division in the primary endosperm cell appears to be longitudinal producing two unequal cells of endosperm. The smaller cell has divided longitudinally while the larger one transversely and further divisions in these cells have been irregular (Fig. 321). Still in another case the division in the primary endosperm cell appears to be longitudinal producing two celled endosperm. The division in both the endosperm cells are irregular (Fig.322). In a four celled endosperm it has been observed that the primary micropylar endosperm chamber has divided longitudinally while the primary chalazal endosperm chamber transversely producing four cells arranged in a T—shaped manner (Fig. 323). In one case it appears that the primary chalazal endosperm chamber has divided transversely (Fig. 324). In another case the division in primary endosperm chambers is transverse resulting in four linearly arranged cells (Fig. 325). The cells in the early stages have vacuolated cytoplasm. Later the cells of the endosperm become densely cytoplasmic and replete with starch grains.

SOLANUM CORNUTUM

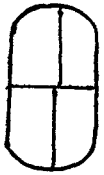
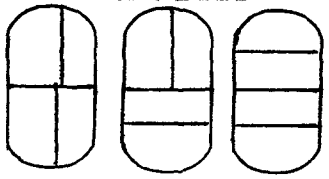
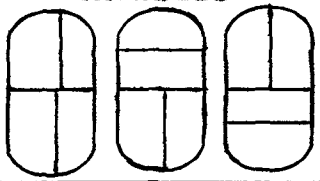
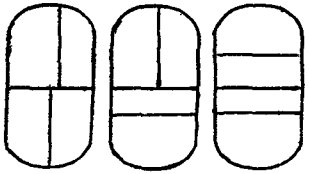
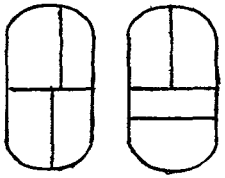
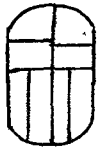
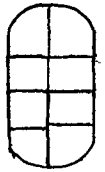
The primary endosperm nucleus divides transversely producing the primary micropylar and primary chalazal endosperm chambers (Figs. 327, 328). The division in either chamber may precede the other (Figs. 329, 330).

Sometimes the division in the primary chalazal endosperm chamber is delayed while the micropylar chamber has produced three cells (Figs. 331, 332). The division in both the endosperm chambers is longitudinal. Thus four celled endosperm is formed (Fig. 333). Further the divisions in the endosperm cells are irregular.

Variations in the plane of divisions in the early stages of endosperm development have been observed. In one case the primary chalazal endosperm chamber may divide transversely while the primary micropylar endosperm chamber has divided longitudinally and the four cells are arranged in a T-shaped manner (Fig. 334). In another case the first division in the primary endosperm cell appears to be longitudinal dividing the embryo sac into two unequal cells. One of the juxtaposed cells has divided transversely and the other longitudinally (Fig. 335). Later, the divisions in the endosperm become irregular and a multicellular endosperm is formed (Fig. 336).

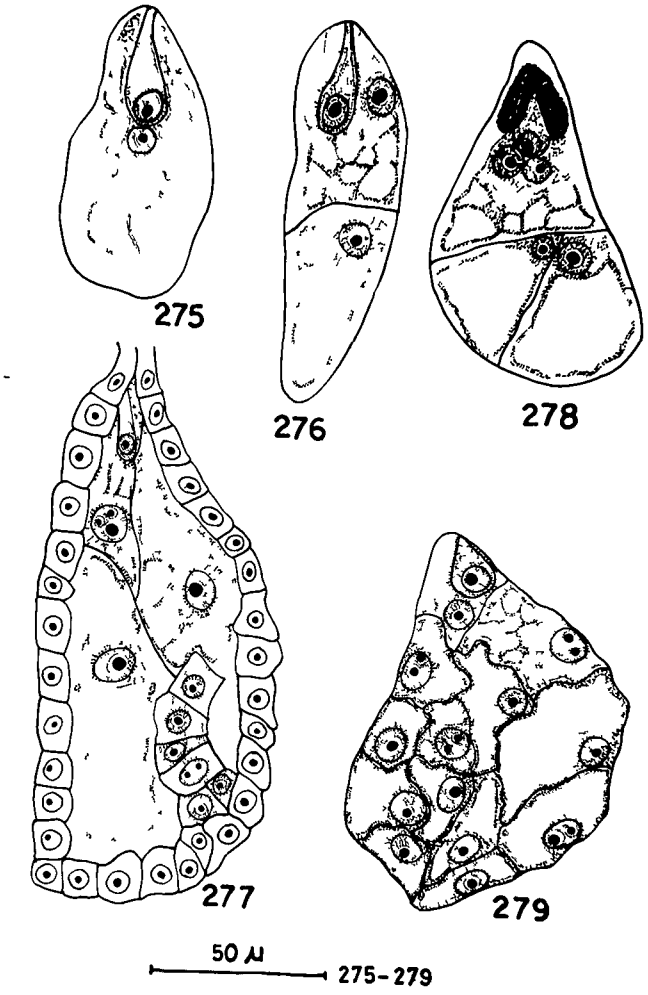
ENDOSPERM

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Endosperm	Cellular	Cellular	Cellular	Cellular	Cellular
First division	Transverse	Transverse Rarely longitudinal	Transverse Rarely oblique	Transverse	Transverse Rarely longitudinal
Second division	Longitudinal in both the primary endosperm chambers 	Longitudinal in both the chambers rarely transverse in chalazal or both the chambers 	Longitudinal in both the chambers rarely transverse in micropylar or chalazal chambers 	Longitudinal in both the chambers rarely transverse in chalazal or both the chambers 	Longitudinal in both the chambers rarely transverse in chalazal chamber 
Third division forming 8-cells	Could not be observed	Longitudinal in micropylar and chalazal chamber 	Transverse in micropylar & longitudinal in chalazal chamber 	Transverse in micropylar & chalazal chambers 	Irregular

EXPLANATION OF FIGURES

Figs. 275-279. Solanum hispidum. Development of endosperm. Fig. 275. L.s. fertilized embryo sac showing zygote and primary endosperm nucleus. Fig. 276. 2-celled endosperm. Fig. 277. 3-celled endosperm and endothelial embryo. Fig. 278. 4-celled endosperm. Fig. 279. Multicellular endosperm.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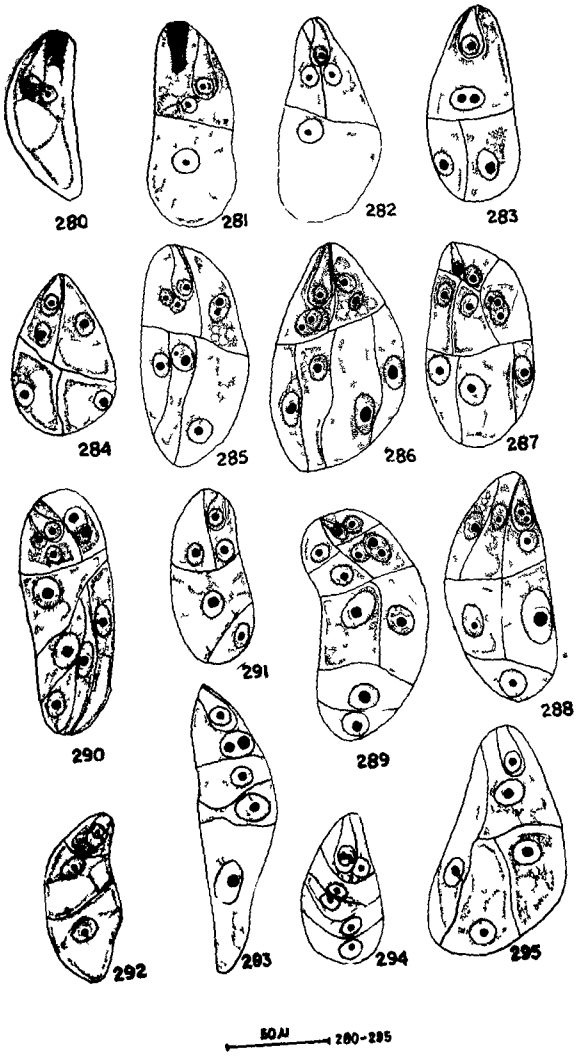
EXPLANATION OF FIGURES

Figs. 280-295. Solanum furcatum. Development of endosperm. Fig. 280. L.s. fertilized embryo sac showing zygote and primary endosperm nucleus. Fig. 281. 2-celled endosperm. Figs. 282, 283. 3-celled endosperm. Fig. 284. 4-celled endosperm. Figs. 285, 286. The cells of the micropylar and chalazal endosperm chambers have divided longitudinally. Fig. 287. 8-celled endosperm. One of the two juxtaposed cells of the micropylar endosperm chamber has divided transversely and the other longitudinally. Fig. 288. 6-celled endosperm. The primary chalazal endosperm chamber had divided transversely. Fig. 289. 9-celled endosperm. The two juxtaposed cells of micropylar endosperm chamber havedivided transversely. Fig. 290. 9-celled endosperm. The primary chalazal endosperm chamber appears to have divided transversely. Fig. 291. 4-celled endosperm showing T-shaped arrangement. Figs. 292-294. 3, 4 and 5-celled endosperm respectively showing linear arrangement. Fig. 295. 4-celled endosperm. The first division in the primary endosperm nucleus has been longitudinal.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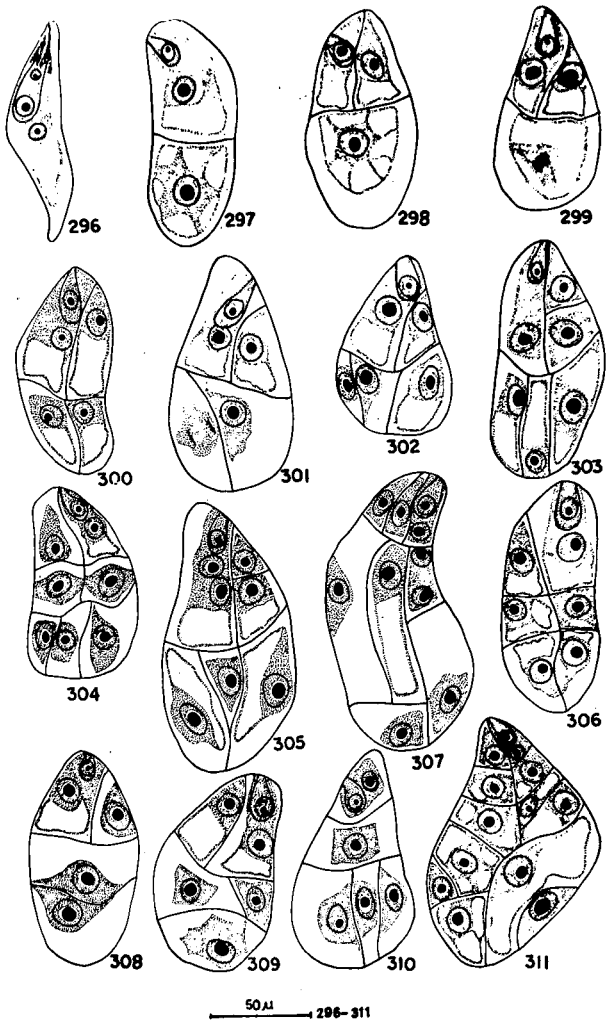
EXPLANATION OF FIGURES

Figs. 296-311. Solanum retroflexum. Development of endosperm. Fig. 296. L.s. fertilized embryo sac showing zygote and primary endosperm nucleus. Fig. 297. 2-celled endosperm. Figs. 298, 299. 3-celled endosperm. Fig. 300. 4-celled endosperm. Fig. 301. 4-celled endosperm. One of the two juxtaposed cells of the chalazal endosperm chamber is dividing longitudinally. Fig. 302. 5-celled endosperm. One of the two juxtaposed cells of chalazal endosperm chamber has divided longitudinally. Figs. 303, 304. 6 and 7-celled endosperm respectively showing transverse division in the cells of the primary micropylar endoschamber. Fig. 305. 7-celled endosperm. One of the juxtaposed cells of the primary micropylar endosperm chamber has divided transversely and the other longitudinally. Fig. 306. 6-celled endosperm; the cells of the chalazal endosperm chamber has divided transversely. Fig. 307. 9-celled endosperm. One of the cells of micropylar endosperm chamber has divided longitudinally. Fig. 308. 4-celled endosperm showing T-shaped arrangement. Fig. 309. 5-celled endosperm developed from T-shaped arrangement. The second cell from chalazal side has divided longitudinally. Fig. 310. 5-celled endosperm. The primary micropylar endosperm chamber has divided transversely. Fig. 311. Multicellular endosperm. The first two divisions in the primary endosperm cell appear to have been longitudinal.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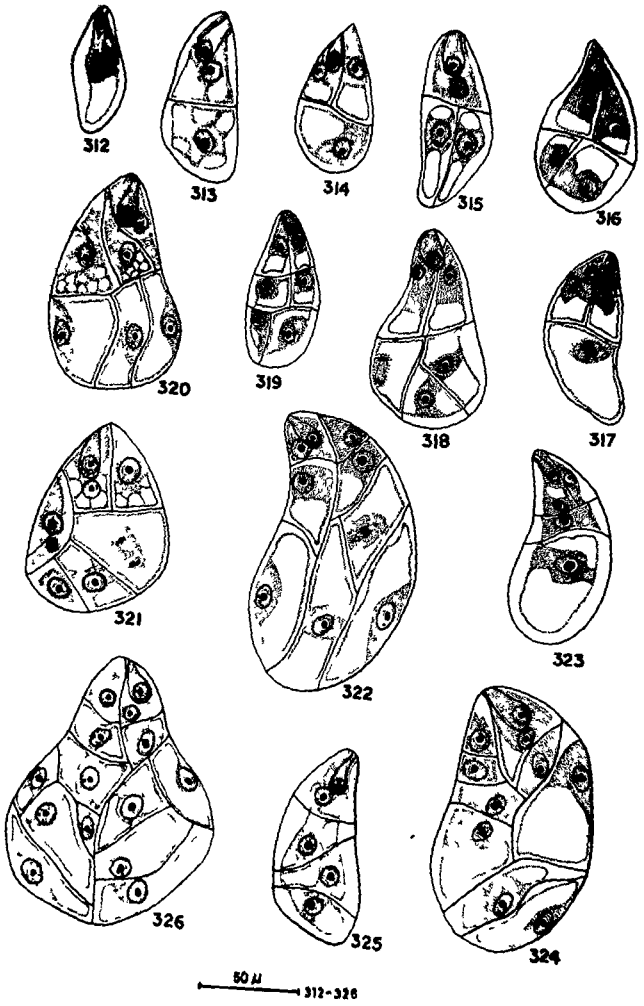
EXPLANATION OF FIGURES

Figs. 312-326. *Solanum douglasii*. Development of endosperm. Fig. 312. L.s. embryo sac showing zygote and primary endosperm nucleus. Fig. 313. 2-celled endosperm. Figs. 314, 315. 3-celled endosperm. Fig. 316. 4-celled endosperm. Fig. 317. 5-celled endosperm. The primary chalazal endosperm endosperm chamber is dividing longitudinally while both cells of the primary micropylar endosperm chamber have divided transversely. Fig. 318. 5-celled endosperm; one of the two juxtaposed cells of chalazal endosperm chamber is dividing while the other has completed division. Fig. 319. 6-celled endosperm. Fig. 320. 6-celled endosperm. The cells of the primary micropylar and primary chalazal endosperm chamber have divided longitudinally. Fig. 321. 7-celled endosperm. The first division in the primary endosperm nucleus appears to have been longitudinal. Fig. 322. 8-celled endosperm. The first two divisions in the primary endosperm endosperm appears to be longitudinal. Fig. 323. 4-celled endosperm showing T-shaped arrangement. Fig. 324. Multicellular endosperm. The primary chalazal endosperm chamber has divided transversely, while the micropylar longitudinally. Fig. 325. 4-celled endosperm showing linear arrangement. Fig. 326. Multicellular endosperm.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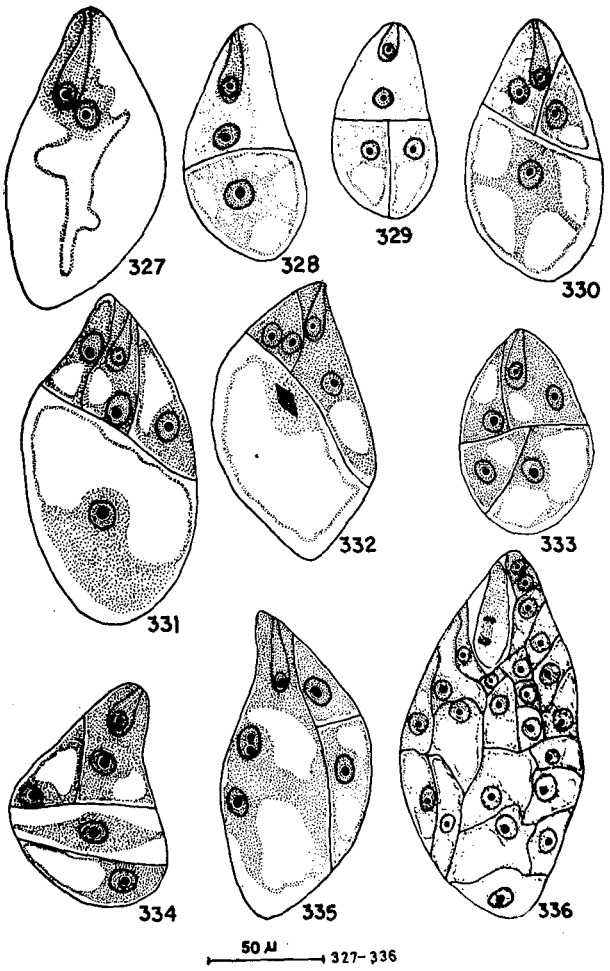
EXPLANATION OF FIGURES

Figs. 327-336. *Solanum cornutum*. Development of endosperm. Fig. 327. L.s. fertilized embryo sac showing zygote and primary endosperm nucleus. Fig. 328. 2-celled endosperm. Figs. 329, 330. 3-celled endosperm. Fig. 331. 4-celled endosperm. One of the juxtaposed cells of primary micropylar endosperm chamber has divided longitudinally. Fig. 332. 4-celled endosperm. The primary chalazal endosperm chamber is dividing longitudinally. Fig. 333. 4-celled endosperm. Fig. 334. 4-celled endosperm showing T-shaped arrangement. Fig. 335. 4-celled endosperm. The primary endosperm nucleus has divided longitudinally, one of the resultant cells divided transversely and the other longitudinally. Fig. 336. Multicellular endosperm.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EMBRYOGENY

The embryogeny in the different species of Solanum is inconsistent. Besides one normal type of embryogeny, sporadic variations which belong to other principal types also may occur in the same species. Thus for the sake of clarity the embryogeny in the species described here has been dealt with separately.

SOLANUM HISPIDUM

Soon after fertilization there is great activity in the development of endosperm but the zygote remains inactive till the endosperm becomes multicellular.

A transverse division in the zygote cuts off an apical cell ca and a basal cell cb (Figs.337, 338).The cell ca divides transversely giving rise to the tiers 1 and 1'. The cell cb also divides in the similar plane to produce m and ci (Fig. 339). Thus at the four celled stage the proembryo has a linear arrangement of its cells (Fig. 339). The division in 1 and 1' is vertical producing quadrants (Figs. 340-342). The upper and lower quadrant cells are in the same plane (Fig. 342).Later,transverse divisions take place in the quadrants and octant stage is formed (Fig. 343). Meanwhile the cell m also divides vertically (Figs. 342, 343). The division in ci is transverse producing n and n' (Figs. 342, 343).Later, repeated divisions in the derivatives of 1 and 1' give rise to a globular proembryo (Fig. 344), which subseque-

ntly differentiates into heart-shaped (Fig. 345), torpedo-shaped (Fig. 346) and finally to a mature slightly curved dicotyledonous embryo (Fig. 354). It appears that the daughter cells of l and l' and m constitute the embryo proper while those of ci give rise to the uniseriate suspensor. Thus the embryogeny in the species conforms to the Myosotis variation of Chenopodiad type.

Variations in the size and number of cotyledons have also been observed. In several cases, one of the cotyledons was fully developed while the other was rudimentary (Figs. 347, 348). In a large number of cases it has been observed that the two cotyledons move in different directions (Figs. 348, 349). Occasionally the embryo may have three cotyledons, which also may move in different directions (Figs. 350, 351). In one case the embryo possesses four rudimentary cotyledons (Fig. 353). In an exceptional case the embryo is somewhat kidney-shaped (Fig. 352).

In addition to zygotic embryo a large number of embryos may arise from the endothelium (Figs. 355 — 359, 361, 362). The endothelium differentiates at 2-nucleate embryo sac stage. Its cells possess prominent nuclei with vacuolated cytoplasm. The endothelium is multiplicative in nature and becomes 1-3 layered after fertilization. Some of the cells of the endothelium proliferate and form embryo like structures which grow inside the embryo sac cavity (Figs. 356-359, 361, 362). There is no definite sequence of divisions of the embryonal cells developed from endothelium. The origin of adventive embryos can be

ascertained by their lateral position and contents similar to those of endothelial cells. The embryos are devoid of true suspensor and could be easily distinguished from the zygotic embryos.

The number of adventive embryos developing from the endothelium is quite variable and sometimes such embryos completely fill the embryo sac cavity (Figs. 361, 362). In such cases the endosperm does not develop further. In one exceptional case it appears that two embryo sacs developed in the same ovule. In one of them normal zygotic linear proembryonic tetrad developed while in the other the cavity of the embryo sac is completely filled with endothelial embryos of irregular shape and size (Figs. 361, 362).

During seed development it has also been observed that sometimes endothelial embryos degenerate while sometimes zygotic embryo degenerates (Fig. 360). The degeneration of zygotic or adventive embryos may be due to lack of proper nutrition as endosperm does not develop where adventive embryos develop. Thus resulting seeds are abortive.

SOLANUM FURCATUM

The embryogeny in Solanum furcatum corresponds to the Nicotiana variation of Solanad type. The zygote divides transversely producing a terminal cell ca and a basal cell cb (Figs. 363, 364). The cell ca and cb di-

vide transversely producing a linear proembryonic tetrad (Figs. 365-367). The cells m and ci divide transversely forming d and f and n and n' respectively (Figs.368-370). The cell n and n' divide transversely producing h, k and o, p respectively (Figs. 370, 371). Thus a uniseriate suspensor composed of about 6-10 cells is formed (Figs. 371, 375). The divisions in the tiers l and l' are variable. Either of them may divide first (Figs. 372, 373). The tiers l and l' divide vertically giving rise to the quadrants (Figs. 372-374). The cells of the quadrants divide longitudinally forming octant stage (Figs.375,376). By repeated divisions of octants the embryo becomes globular in shape (Figs. 377, 378). The globular embryo subsequently differentiates into heart-shaped (Fig.381) and finally to a mature strongly curved dicotyledon—ous embryo (Fig. 382).

Sometimes the cell ca may divide longitudinally producing two juxtaposed cells, g and cb transversely producing m and ci. Thus the proembryonic tetrad is L-shaped (Fig. 379). One of the daughter cells of g divides vertically while the other transversely producing the quadrant cells (Fig. 380). Further stages of this type of embryogeny could not be observed successfully. However, it appears that the embryogeny sometimes conforms to the Ruta variation of Onagrad type.

SOLANUM RETROFLEXUM

The zygote divides transversely forming a terminal cell ca and a basal cell cb (Figs. 383, 384). The division in cb precedes that in ca (Figs. 385, 386). The cells ca and cb divide transversely to give rise to l and l' and m and ci respectively. Thus a linear proembryonic tetrad is formed (Fig. 387). The cells m and ci divide transversely producing d and f and n and n' respectively (Figs. 388, 389). Thus a uniseriate suspensor composed of 5-7 cells is formed (Figs. 390,393). The divisions either precede in l or l'(Figs. 391,392). The divisions in l and l' are vertical to give rise to the quadrants (Figs. 391-393). The cells of quadrant divide vertically forming an octant stage (Figs. 394-398). Later, repeated divisions occur in octants and the embryo becomes globular in shape (Figs. 399 —401). The globular proembryo subsequently differentiates into heart-shaped (Fig. 405), torpedo-shaped (Fig. 406) and finally to a curved dicotyledonous embryo (Figs. 407, 408). Thus the embryogeny in S.retroflexum conforms to the Nicotiana variation of Solanad type.

Sometimes the cell m divides vertically and contributes to the embryo proper (Figs. 395, 397). Thus the embryogeny sometimes conforms to Myosotis variation of Chenopodiad type.

Rarely the proembryonic tetrad may be T-shaped(Fig. 402). One of the daughter cells of g divides vertically

while the other transversely producing the quadrant cells (Figs. 403, 404). Thus the embryogeny sometimes conforms to the Ruta variation of Onagrad type.

SOLANUM DOUGLASII

The embryogeny in S. douglasii conforms to the Nicotiana variation of Solanad type. The first division in the zygote is transverse producing an apical cell ca and a basal cell cb (Figs. 409, 410). The division in cb precedes that in ca (Fig. 411). The cell ca divides trasversely to give rise to l and l'. The cell cb also divides in a similar plane producing the cells m and ci. Thus a linear proembryonic tetrad is formed (Fig.412). The cell m and ci divide transversely producing a long suspensor. The tiers l and l' divide by vertical walls forming a quadrant stage (Figs. 413, 414). The quadrant cells divide longitudinally forming an octant stage(Fig. 415, 416). Further divisions in the tiers l and l' give rise to a globular proembryo (Figs. 417, 418), which subsequently differentiates into heart-shaped (Fig.419) and finally to a mature curved dicotyledonous embryo (Fig. 420).

SOLANUM CORNUTUM

The zygote divides transversely resulting in an apical cell ca and a basal cell cb (Figs. 421-423). The division in cb precedes that in ca (Fig. 424). The cell ca divides transversely giving rise to the tiers l and

l' (Fig. 425). The cell cb also divides in a similar plane to produce m and ci. Thus at the four celled stage the proembryo has a linear disposition of its cells (Fig. 425). The cell ci divides transversely giving rise to a 5-celled linear proembryo (Fig.426). The division in l' precedes that in l (Fig. 427).The division in the tiers l and l' is vertical producing quadrants (Fig. 428). The divisions in quadrants are vertical (Figs. 429, 430). The cell m also divides vertically and contributes in the development of embryoproper (Figs. 429, 430). Further divisions are irregular forming globular proembryo (Fig. 431). The globular proembryo elongates and become pear-shaped with long uniseriate suspensor (Fig. 434). Finally the pear-shaped embryo gives rise to a curved dicotyledonous embryo (Fig. 435). Thus the embryogeny in the species belongs to Myosotis variation of Chenopodiad type.

Rarely the proembryonic tetrad may be T-shaped (Fig. 432). One of the daughter cells of g divides vertically while the other transversely producing the quadrant cells (Fig. 433). Thus the embryogeny may rarely conform to the Ruta variation of Onagrad type.

In an exceptional case it has been observed that the antipodal cells divide, redivide and form an undifferentiated embryonal mass of cells at the chalazal end of the embryo sac (Fig. 436). The two nuclei near the egg could be the two male gametes (Fig. 436). The

further fate of antipodal embryo could not be determined.

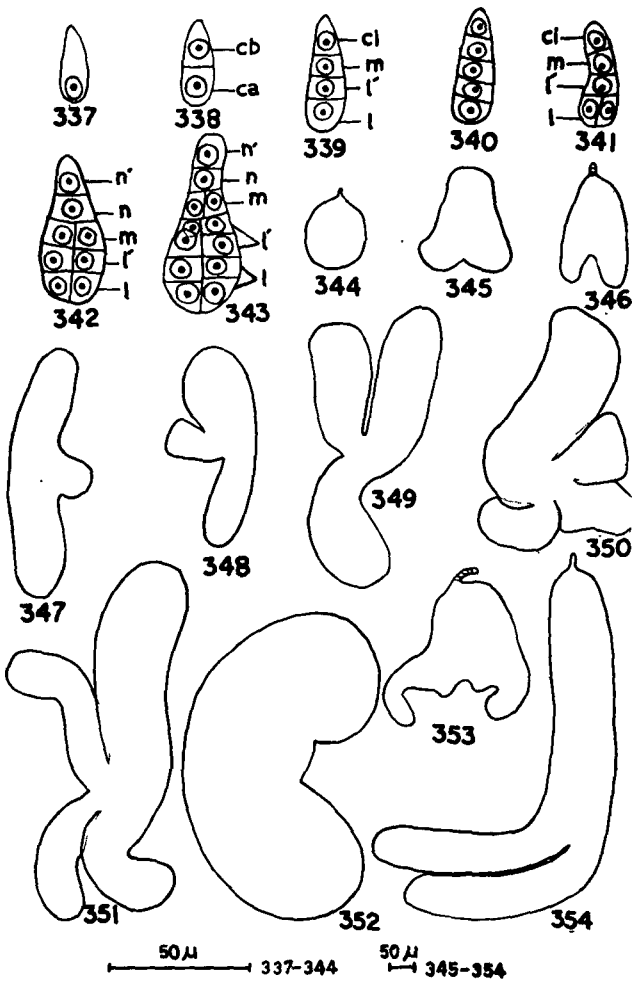
EMBRYOGENY

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Proembryonic tetrad	Linear	Linear sometimes T-shaped	Linear Rarely T-shaped	Linear	Linear Rarely T-shaped
Embryogeny	Myosotis variation Chenopodiad type	Nicotiana variation Solanad type Sometimes Ruta variation Onagrad type	Nicotiana variation Solanad type Sometimes Myosotis variation Chenopodiad type	Nicotiana variation Solanad type	Myosotis variation Chenopodiad type Rarely Ruta variation Onagrad type
Mature embryo	Dicotyledonous Rarely upto four cotyledons	Dicotyledonous	Dicotyledonous	Dicotyledonous	Dicotyledonous
Polyembryony	Adventive embryos developed from endothelium	Absent	Absent	Absent	Antipodal embryo

EXPLANATION OF FIGURES

Figs. 337-354. *Solanum hispidum*. Embryogeny. Fig. 337. Zygote. Fig. 338. 2-celled proembryo. Fig. 339. Linear proembryonic tetrad. Fig. 340. 5-celled proembryo. Fig. 341. Linear proembryonic tetrad. The tier *l* has divided longitudinally. Fig. 342. 8-celled proembryo. The tiers *l* and *l'* and *m* have divided longitudinally. Fig. 343. Octant stage of proembryo. Fig. 344. Globular proembryo. Fig. 345. Heart-shaped embryo. Fig. 346. Torpedo-shaped embryo. Figs. 347, 348. Mature embryo showing one rudimentary cotyledon. Fig. 349. Mature embryo cotyledons developed in different directions. Figs. 350, 351. Embryos with three cotyledons. Fig. 352. Kidney shaped embryo with two cotyledons. Fig. 353. Embryo with four cotyledonary initials. Fig. 354. Mature dicotyledonous embryo.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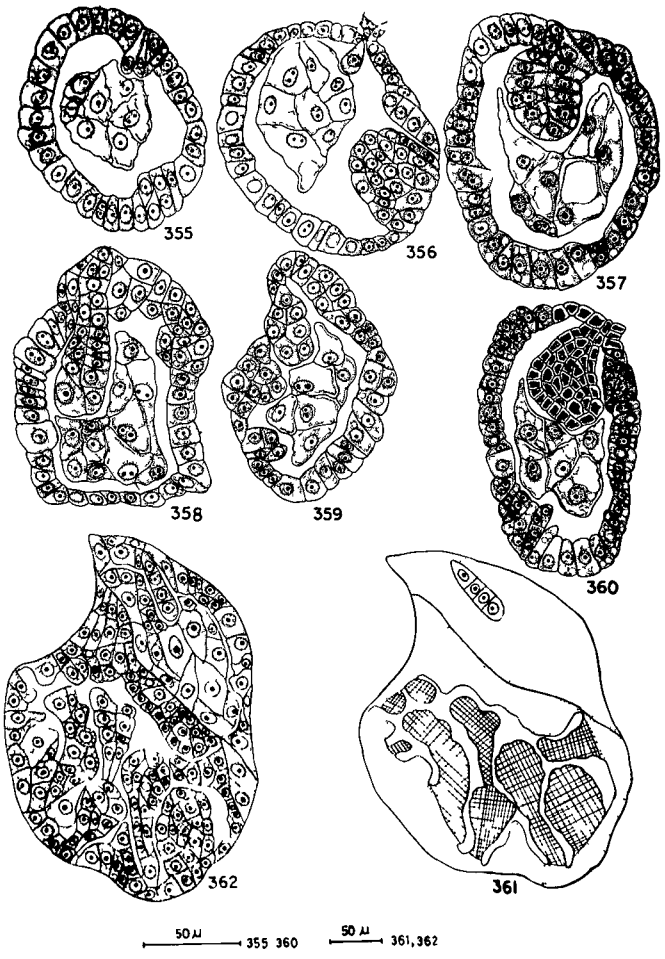
EXPLANATION OF FIGURES

Figs. 355-362. Solanum hispidum. Polyembryony. Fig. 355. L.s. part of fertilized ovule showing zygote, endosperm and endothelium. Fig. 356. L.s. of fertilized sac showing zygote and embryo developed from endothelium. Figs. 357, 358. L.s. embryo sacs showing embryos developed from endothelial cells. Fig. 359. L.s. old sac showing three endothelial embryos. Fig. 360. L.s. sac showing degenerated endothelial embryo. Figs. 361, 362. L.s. part of old ovule showing twin sacs; one sac shows linear proembryonic tetrad developed from zygote and endosperm while the other sac has many endothelial embryos.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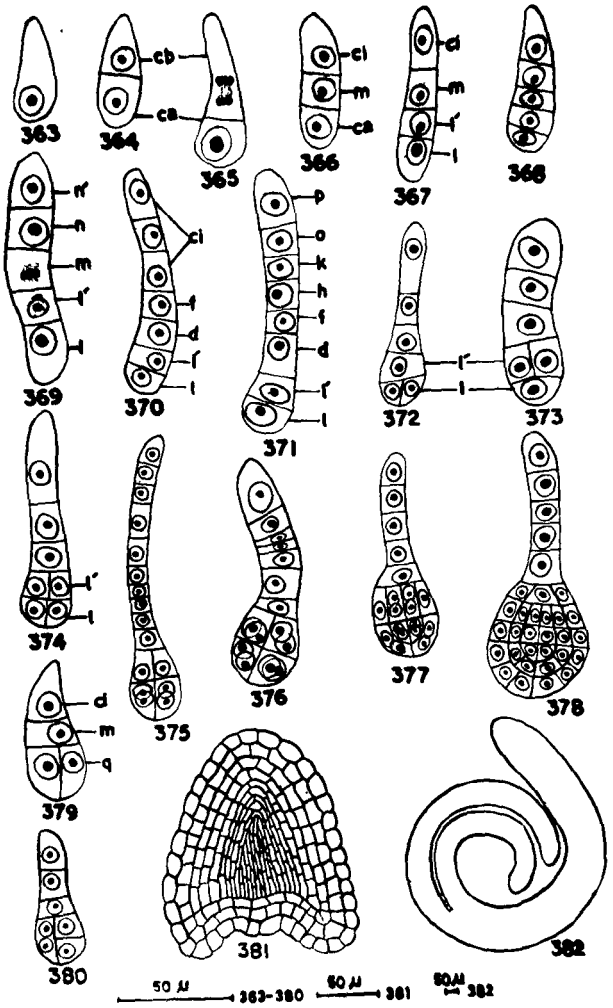
EXPLANATION OF FIGURES

Figs. 363-382. *Solanum furcatum*. Embryogeny. Fig. 363. Zygote. Fig. 364. 2-celled proembryo. Fig. 365. 2-celled proembryo, the cell *cb* is dividing. Fig. 366. 3-celled proembryo. Fig. 367. Linear proembryonic tetrad. Fig. 368. 5-celled linear proembryo. Fig. 369. 5-celled proembryo. The cell *m* is dividing. Fig. 370. 7-celled linear proembryo. Fig. 371. 8-celled linear proembryo. Fig. 372. 6-celled proembryo. The tier *l* has divided. Fig. 373. 6-celled proembryo. The tier *l'* has divided. Fig. 374. Quadrant stage of proembryo. Fig. 375. 16 celled proembryo. There are four daughter cells of *l* and two of *l'*. Fig. 376. Octant stage of proembryo. Fig. 377. Post octant stage of proembryo. Fig. 378. Globular stage of proembryo. Fig. 379. T— shaped proembryonic tetrad. Fig. 380. T-shaped proembryo-nic tetrad; one of the juxtaposed cells of *g* has divided longitudinally while the other transversely. Fig. 381. Heart-shaped proembryo. Fig. 382. Mature dicotyledon— ous curved embryo.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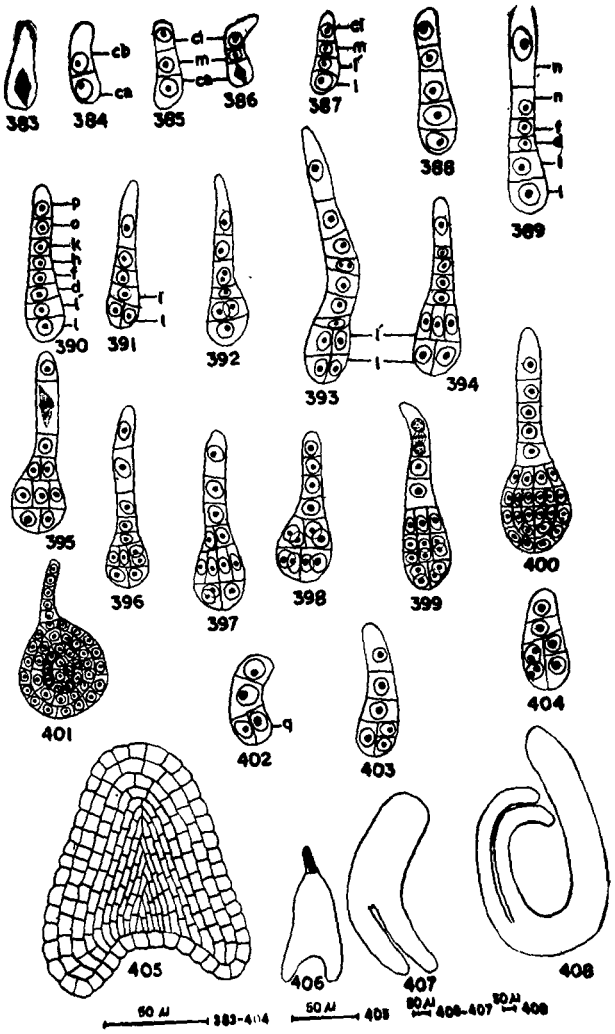
EXPLANATION OF FIGURES

Figs. 383-408. Solanum retroflexum. Embryogeny. Fig. 383. Zygote. Fig. 384. 2-celled proembryo. Fig. 385. 3-celled proembryo. Fig. 386. 3-celled proembryo, ca is dividing Fig. 387. Linear proembryonic tetrad. Fig. 388. 5-celled linear proembryo. Fig. 389. 6-celled linear proembryo. Fig. 390. 8-celled linear proembryo. Fig. 391. 6-celled proembryo showing longitudinal division in l. Fig. 392. 6-celled proembryo, the tier l' has divided longitudinally. Fig. 393. Quadrant stage of proembryo. Fig. 394. 10-celled proembryo. There are three daughter cells of l' and two of l. Fig. 395. 10-celled proembryo. There are three daughter cells of l' and two of l. The cell m has divided longitudinally. Fig. 396. 11-celled proembryo. There are two cells of l and four cells of l'. Figs. 397, 398. Almost octant stages of proembryos respectively. Fig. 399. Post octant stage of proembryo. Figs. 400, 401. Globular stage of proembryo. Fig. 402. T-shaped proembryonic tetrad. Fig. 403. One of the juxtaposed cells of g has divided transversely. Fig. 404. T-shaped proembryo showing one of the juxtaposed cells of g has divided longitudinally while the other transversely. Fig. 405, 406. Heart shaped embryo. Fig. 407. Torpedo shaped embryo. Fig. 408. Mature dicotyledonous embryo.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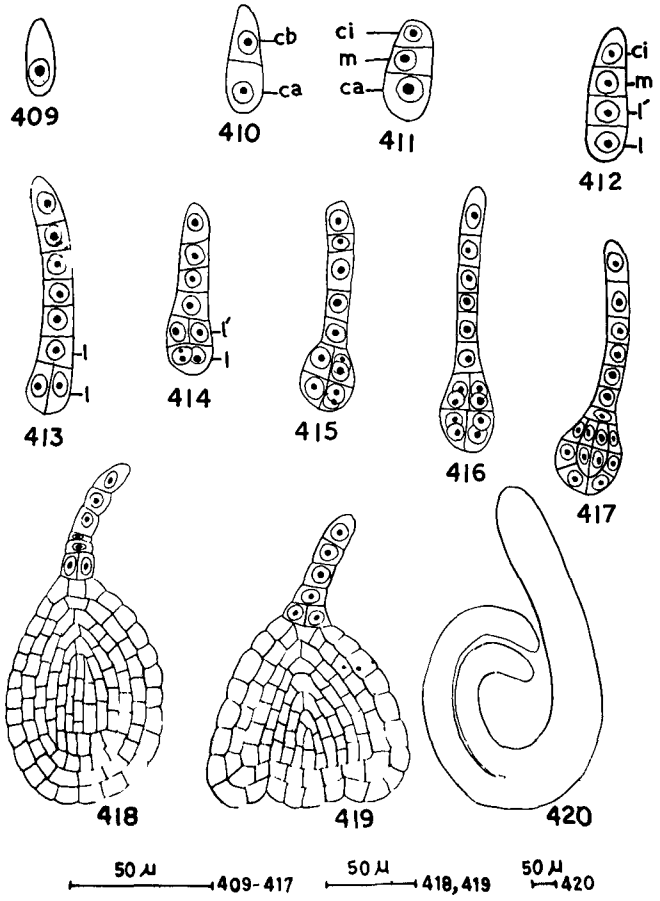
EXPLANATION OF FIGURES

Figs. 409-420. Solanum douglasii. Embryogeny. Fig. 409. Zygote. Fig. 410. 2-celled proembryo. Fig. 411. 3-celled proembryo. Fig. 412. Linear proembryonic tetrad. Fig. 413. 8-celled proembryo. The tier $\underline{1}$ has divided longitudinally. Fig. 414. Quadrant stage of proembryo. Fig. 415. 11-celled proembryo. There are three daughter cells of $\underline{1}$ and three of $\underline{1}'$. Fig. 416. Octant stage of proembryo. Fig. 417. Post octant stage of proembryo. Fig. 418. Globular proembryo. Fig. 419. Heart-shaped embryo. Fig. 420. Mature dicotyledonous curved embryo.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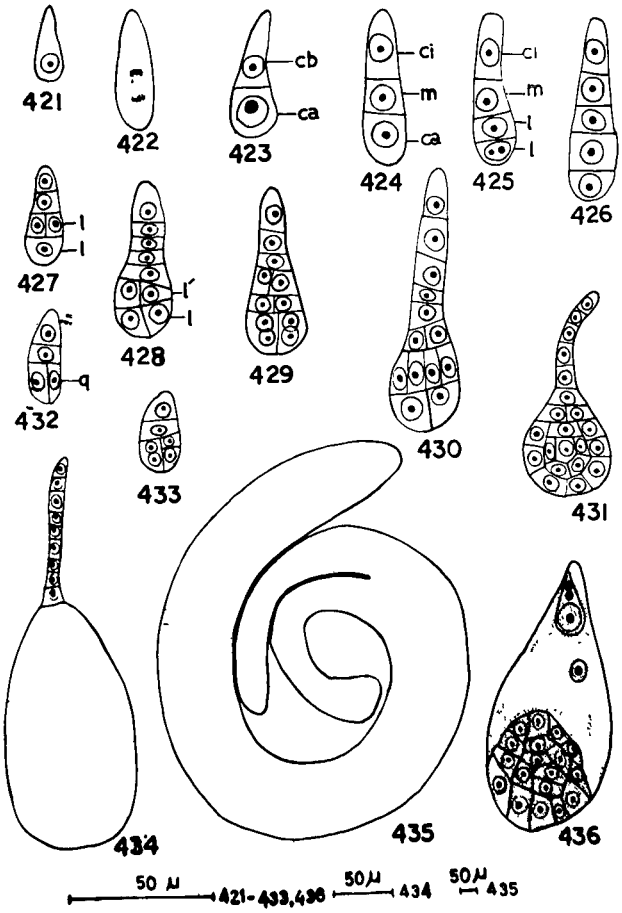
EXPLANATION OF FIGURES

Figs. 421-436. *Solanum cornutum*. Embryogeny. Fig. 421. Zygote. Fig. 422. Zygote at anaphase stage. Fig. 423. 2-celled proembryo. Fig. 424. 3-celled proembryo. Fig. 425. Linear proembryonic tetrad. Fig. 426. 5-celled linear proembryo. Fig. 427. Linear proembryonic tetrad. The tier l' has divided longitudinally. Fig. 428. Quadrant stage of proembryo. Fig. 429. 11-celled proembryo. The cell m has divided longitudinally. There are four daughter cells of l and two of l'. Fig. 430. 13-celled proembryo. There are two daughter cells of l and six of l'. The cell m has also divided longitudinally. Fig. 431. Globular proembryo. Fig. 432. T-shaped proembryonic tetrad. Fig. 433. T-shaped proembryonic tetrad; one of the juxtaposed cells of q has divided longitudinally while the other transversely. Fig. 434. Pear-shaped proembryo with a long suspensor. Fig. 435. Mature dicotyledonous curved embryo. Fig. 436. Embryo sac showing zygote, primary endosperm nucleus and embryo formed from the antipodal cells.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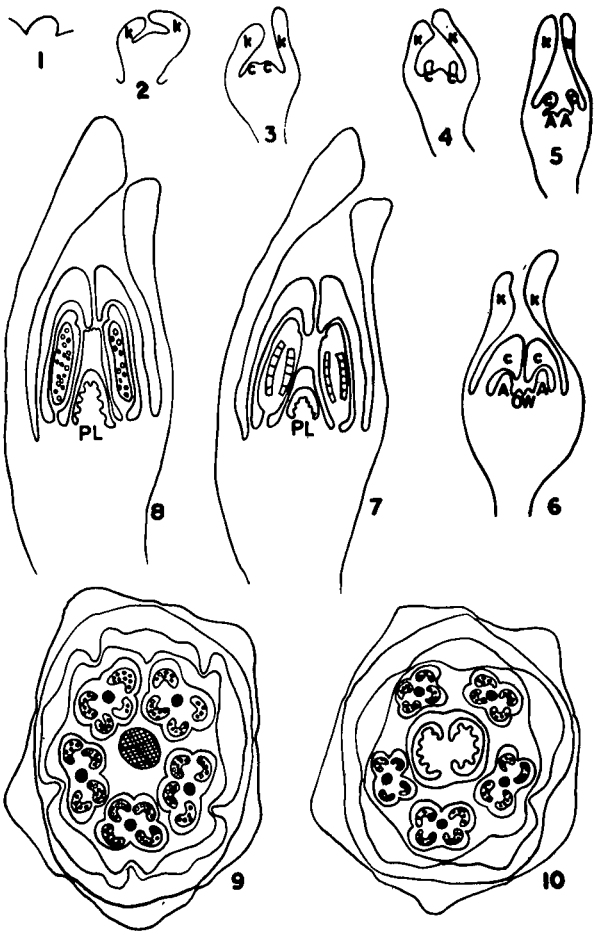

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SEED

The species of Solanum described in the present study show considerable differences in the structure and development of seed, therefore, have been dealt with separately.

SOLANUM HISPIDUM

The ovules are anatropous, unitegmic and tenuinucellate. The integument in the early stages of ovule development is composed of 4-5 layers of cells. Later the integument becomes appreciably thick due to addition of several layers of cells formed by repeated divisions of the hypodermal cells. The nucellus degenerates at the 2-nucleate embryo sac stage. The integument at mature embryo sac stage is 7-9 layered while it becomes 20-22 layered at zygote stage (Fig. 437). The innermost layer of the integument differentiates into endothelium, whose cells are generally radially elongated, uninucleate with vacuolated cytoplasm. The cells of endothelium divide mitotically and become 2-4 layered (Figs. 438-441). At the octant stage of proembryo the layers of the integument increase and become 24-25 (Fig. 439). The endothelium persists and forms the innermost layer of the seed coat.

The developing endosperm encroaches upon the integumental cells. Thus at the mature seed stage the cells of the integument are completely disorganized. Concurrently the epidermal cells enlarge and become heavily lignified, which show sclerotic thickenings in the inner portion but

their radial walls in the outer region develop fibrous thickenings.

The seed coat at mature seed stage comprises the epidermis, which forms the main protective layer and 3-4 layers of the endothelium (Figs. 440, 441). The cells of the endothelium may be pentagonal, hexagonal or irregularly shaped. The cells of the endothelium lose their contents and their walls become lignified. The walls of the endosperm cells become thick due to the deposition of cellulose. The cells of the endosperm possess starch grains and reserve food material (Fig. 441). The developing embryo consumes considerable amount of endosperm and at the mature seed stage only few layers of endosperm persist towards periphery.

The mature seeds are kidney-shaped and consistsof a single layered epidermis, persistent 3-4 layered endothelium, few layers of endosperm and a curved dicotyledonous embryo (Fig. 440).

SOLANUM FURCATUM

The ovules in Solanum furcatum are unitegmic. The integument is composed of 3-4 cell layers at the megaspore mother cell stage. The cells of the integu—ment divide periclinally and the integument becomes 5—7 celled thick at the mature embryo sac stage. The nucellus disappears at the 2-nucleate embryo sac stage. The innermost layer of the integument differentiates as endothelium. The endothelial cells stretch and become tangentially flattened in developing seeds. The endo-

thelial cells are uninucleate with vacuolated cytoplasm. In fertilized ovules the number of cell layers of integument increases and becomes 12-18 layered at quadrant stage (Fig. 442). The endosperm grows in size and encroaches upon the integumental cells, thus the cells lying adjacent to the endothelium are crushed. Mean while the endothelial cells also start degeneration at the globular stage of proembryo (Fig. 443). The epidermal cells enlarge and develop sclerotic thickenings at the inner portion while the outer regions develop only rod like fibrous thickenings (Fig. 445).

The seed coat at the mature stage of embryo comprises the epidermis, which forms the main mechanical protective layer. Most of the endosperm is absorbed by the developing embryo and only few layers persist in the mature seed. The cells of endosperm possess reserve food materials.

The mature seeds are small kidney-shaped compressed and consist of a seed coat, persistent endosperm and a curved dicotyledonous embryo (Fig. 444).

SOLANUM RETROFLEXUM

The ovules are anatropous, unitegmic and tenuinucellate. The integument at the megaspore mother cell stage comprises 4-5 cell layers, which become 6-7 layered at the organized embryo sac stage. The cells of the innermost layer of the integument enlarge and differentiates as endothelium. These cells remain uninucleate and possess vacuolated cytoplasm. The endothelial cells are

tangentially flattened in developing seeds. The number of cell layers of the integument at 3-celled proembryo increases and becomes 13-14 (Fig. 446). The cells outside the endothelium are tangentially flattened and compressed due to pressure developed by developing endosperm. The cells of the integument just below the epidermis are fairly large (Fig. 446). The growth in the cell layers of integument continues and the integument becomes 18-20 layered at 10-celled proembryo (Fig.447). The cells of the endosperm grow in size and encroach upon the integumental cells and the cells lying adjacent to the endothelium are absorbed.

At the globular stage of proembryo the endothelial cells start degeneration. During the further development of seed the cells of integument are absorbed and their absorption progresses from inside to outside and only 5-8 layers persist in the mature seed (Fig. 449). The epidermal cells enlarge and become heavily lignified. The inner portion of the epidermal cells possesses sclerotic type of thickenings and fibrous thickenings develop in the outer region of the cells.

Anatomically the seed comprises epidermis, 5-8 layers of integument, persistent endosperm and mature curved dicotyledonous embryo (Fig. 448). The seed coat consists of an epidermis which forms the main protec—tive layer and 5-8 compressed layers of integument (Fig.449). Sometimes the epidermis at places becomes 2-layered (Fig. 450). The endosperm cells are thin walled and

occupy a large portion of interior space of the seed. It extends between the coiled embryo and this part of the endosperm is characterized by a bulbous comma head and a slender comma stem (Fig. 448). The cells of the endosperm possess starch grains and reserve food material.

The mature seeds are kidney-shaped and endospermic with a dicotyledonous embryo (Fig. 448).

SOLANUM DOUGLASII

The ovule in Solanum douglasii is unitegmic, which is 6-7-celled thick at the megaspore mother cell stage. The integument on the free side in the middle region is 8-9 celled thick at the mature embryo sac stage. The cells of the innermost layer of the integument differentiat-es into endothelium. Simultaneously these cells enlarge and become rich in cytoplasmic contents. The endothelial cells are uninucleate, tangentially flattened and persistent. During the seed development number of cell layers of the integument increases and becomes 10-12 at the octant stage of proembryo (Fig. 451). Gradually the cells of the integument are destroyed due to the pressure exerted by enlarging endosperm cells. The endosperm cells possess starch grains and reserve food material (Figs. 455, 456). The cells of the endosperm become thick walled due to the deposition of cellulose. At the mature embryo stage, 2-4 layers of integument persist (Figs. 454, 455). However in a completely mature seed the cells of integument are completely disorganized (Fig. 456).

The seed coat is differentiated into epidermis and single layered endothelium, which persists and forms the innermost layer of seed coat (Fig. 456). The epidermal cells of the seed coat enlarge and provide mechanical support. In a longitudinal section the sclerotic thickenings on the inner tangential wall of epidermal cells are seen upto one third of the cell lumen. At places the cells of the epidermis divide periclinally to form 2-3 layers (Figs. 452, 453). In such cases the sclerotic thickenings are seen only in the inner layer (Fig. 455). The persistent endothelium also develops fibrillar thickenings at the mature seed stage.

SOLANUM CORNUTUM

The ovule in Solanum cornutum is unitegmic. The integument is 4-5 celled thick at the megaspore mother cell stage. The cells of the integument divide periclinally and become 9-10 celled thick at mature embryo sac stage. The nucellus degenerates at 2-nucleate embryo sac stage. The innermost layer of the integument differentiates as endothelium. It is single layered, uninucleate with vacuoleted cytoplasm.

In fertilized ovule the number of cell layers of the integument increases and becomes 12-15 at octant stage of proembryo (Fig. 457). The cells of the endosperm grow in size and encroach upon the integumental cells, thus the cells lying adjacent to the endothelium are crushed and absorbed. The endothelium also starts

disintegration. The cells of the endosperm are thin walled. Most of the layers of the endosperm are consumed by the developing embryo and only few layers persist. The cells possess starch grains and reserve food material.

The epidermal cells enlarge and develop sclerotic thickenings at the inner side of the cells and bear fibrous rod like thickenings in the outer region (Fig. 459). The outer tangential walls of the epidermal cells break and a number of vertical projections grow from the base of each protective cell which appears radially elongated (Fig. 460).

The mature seeds are kidney-shaped with shrinked seed coat brownish black in colour. The seed consists of single layered epidermis, few layers of endosperm and dicotyledonous curved embryo (Fig. 458).

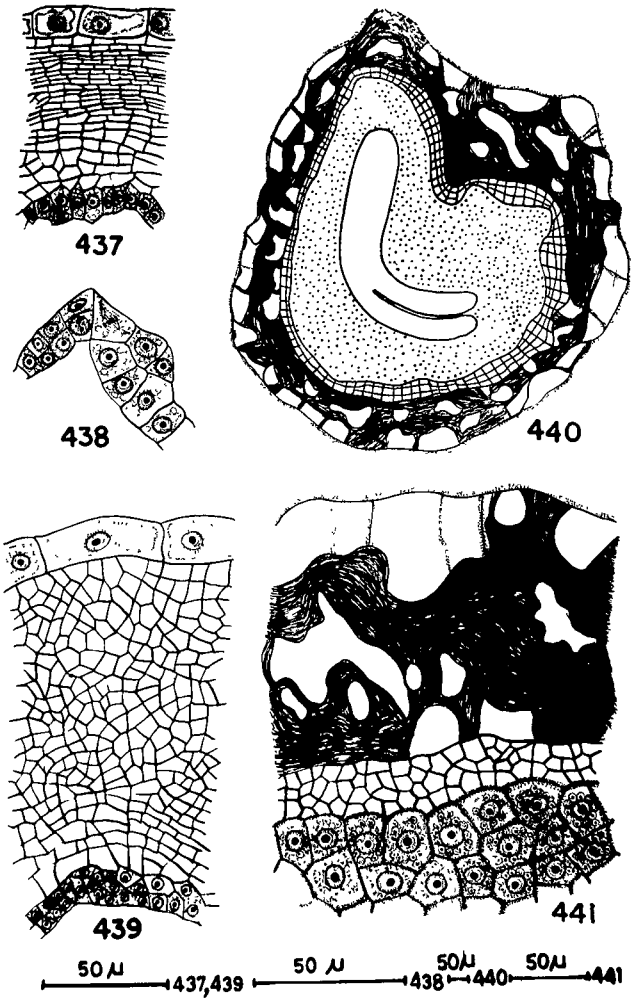
SEED

DISTINGUISHING CHARACTERS

Characters	S. hispidum	S. furcatum	S. retroflexum	S. douglasii	S. cornutum
Seed comprises	Seed coat endosperm embryo	Seed coat endosperm, which extend between coiled embryo. This part of endosperm is characterized by a bulbous coma head and a slender coma stem, embryo	Seed coat endosperm embryo	Seed coat endosperm embryo	Seed coat endosperm embryo
Seed coat comprises	Single-layered epidermis lignified 3-4 layered persistent endothelium	Single layered epidermis	Single layered epidermis at places becomes 2-layered and 5-8 cell layers of integument	Single layered epidermis at places becomes 2-3-layered and fibrous endothelium	Single layered epidermis

EXPLANATION OF FIGURES

Figs. 437-441. *Solanum hispidum*. Development of seed. Fig. 437. L.s. part of ovule at zygote stage showing 23-24 cell layers of integument. Fig. 438. 2-layered endothelium. Fig. 439. L.s. part of seed showing multilayered endothelium and 23-25 layers of integument at octant stage. Fig. 440. L.s. of mature seed showing epidermis, persistent multi-layered endothelium, endosperm and mature dicotyledonous embryo. Fig. 441. L.s. part of mature seed showing thickenings in the epidermis, multi-layered endothelium with lignified walls and starchy endosperm.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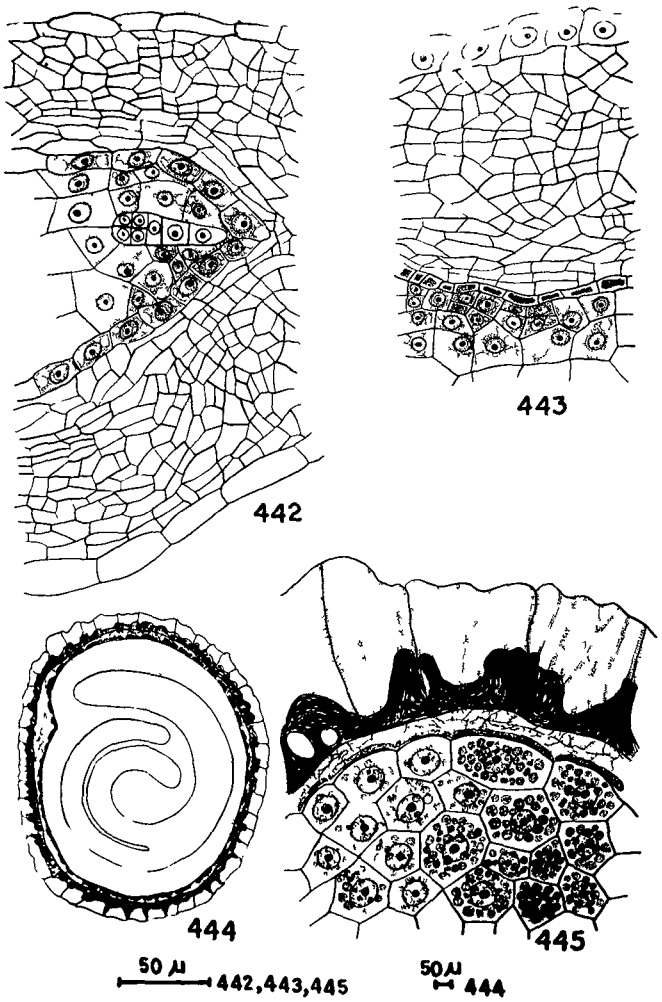
EXPLANATION OF FIGURES

Figs. 442-445. *Solanum furcatum*. Development of seed. Fig. 442. L.s. part of old ovule at quadrant stage of proembryo showing 15-16 celled thick integument and endothelium. Fig. 443. L.s. part of old ovule showing 16-17 layers of integument, degenerating endothelium and endosperm. Fig. 444. L.s. of mature seed showing epidermis, persistent endosperm and dicotyledonous embryo. Fig. 445. L.s. part of mature seed showing thickenings in the epidermis and endosperm.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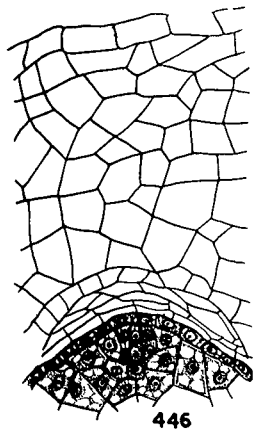
EXPLANATION OF FIGURES

Figs. 446-450. Solenum retroflexum. Development of seed. Fig. 446. L.s. part of ovule showing 13-14 layers of integument, endothelium and 3-celled proembryo. Fig. 447. L.s. part of ovule showing 15-16 layers of integument at young embryo stage. Fig. 448. L.s. of mature seed showing epidermis, 5-8-layers of integument, endosperm and dicotyledonous curved embryo. Fig. 449. L.s. part of mature seed showing thickenings in the epidermis, 5-8 layers of integument and endosperm. Fig. 450. L.s. part of mature seed coat showing 2-layered epidermis.



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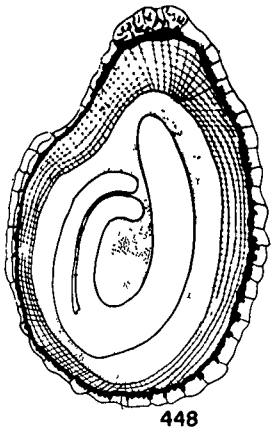

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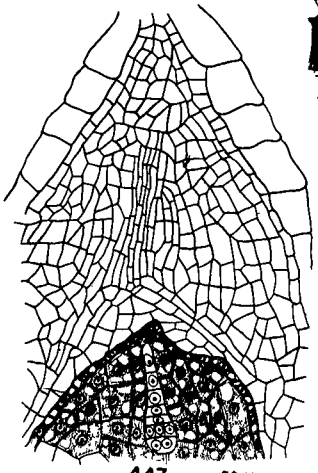

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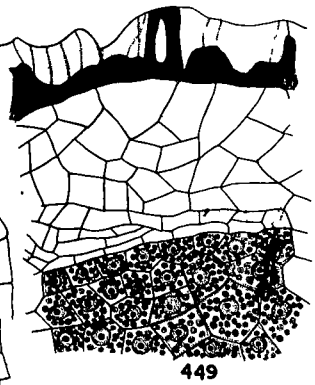

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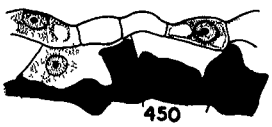

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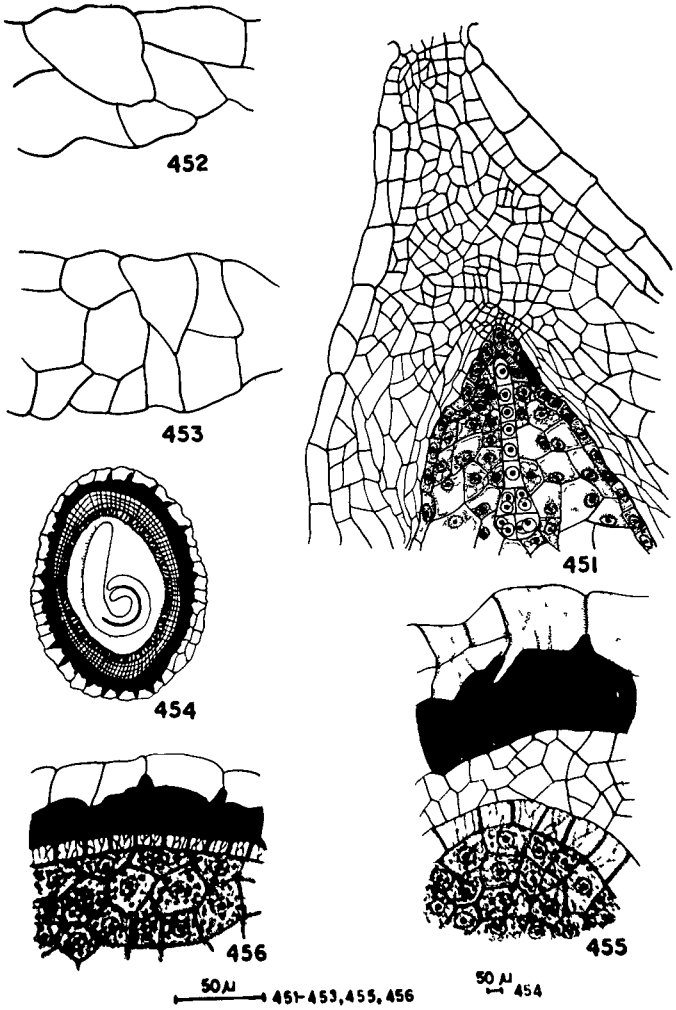
448

EXPLANATION OF FIGURES

Figs. 451-456. *Solanum douglasii*. Development of seed. Fig. 451. L.s. part of seed showing 12-13 layers of integument, persistent endothelium at octant stage of proembryo. Figs. 452, 453. L.s. part of ovule showing 2 and 3-layered epidermis respectively. Fig. 454. L.s. of mature seed showing epidermis, few layers of integument, persistent endothelium, endosperm and mature dicotyledonous curved embryo. Fig. 455. L.s. part of mature seed showing 2-layered epidermis with sclerotic thickenings, 2-3 layers of integument, persistent endothelium with fibrous thickenings and endosperm. Fig. 456. L.s. part of mature seed showing thickenings in the epidermis, persistent endothelium with fibrous thickenings and endosperm.


452
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50 µ
451-453, 455, 456
50 µ
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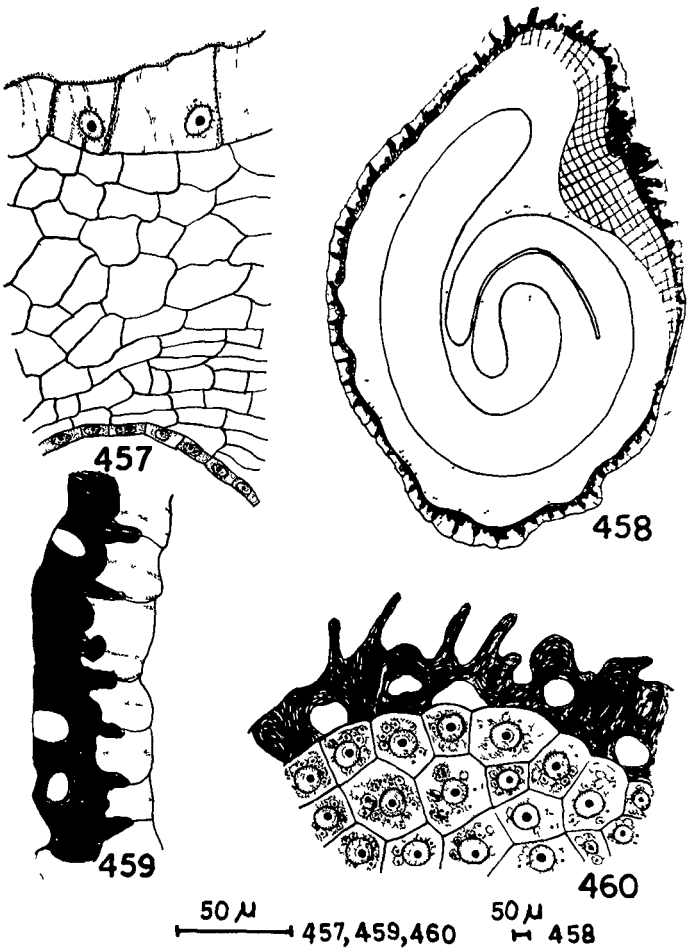
EXPLANATION OF FIGURES

Figs. 457-460. Solanum cornutum. Development of seed. Fig. 457. L.s. part of old ovule at quadrant stage of proembryo showing 16-17 layers of integument and endothelium. Fig. 458. L.s. mature seed showing epidermis, few layers of integument at the micropylar region, endosperm and mature dicotyledonous curved embryo. Fig. 459. L.s. epidermis of seed showing sclerotic and fibrous thickenings. Fig. 460. L.s. part of seed showing epidermis and starchy endosperm.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DISCUSSION

The present discussion is confined to some general remarks about the order Tubiflorae as a whole and the interesting embryological features of the investigated species of Solanum.

The flowers in the Tubiflorae are bisexual, actinomorphic or more often zygomorphic, tetracyclic and hypogynous. In primitive members, the flowers are actinomorphic, tetracyclic and isostemenous while in the highly evolved ones they are zygomorphic with reduction in the number of stamens, carpels, placenta and ovules. From the regular isostemenous flowered families several lines of specialization are discernible. In the Polemoniaceae the flowers are pentamerous and regular, the ovary is tricarpellary and sometimes bicarpellary. The number of ovules varies from numerous to solitary; the position of micropyle resembles that in Convolvulaceae. Hydrophyllaceae recall Polemoniaceae in the plan of the regular flower, but the ovary is usually bicarpellary and bilocular. The reduction in the number of stamens and the number of ovules per carpel is seen in Verbenaceae and Labiatae. The other line of evolution is seen in the suborder Solaninae. It may be traced from the Nolanaceae in which all the five stamens are of equal length and fertile; the ovary is pentacarpellary and 5-10 locular with several ovules in each locule. It is closely allied to the Solanaceae.

The flowers in Solanaceae are pentamerous, actinomorphic, isostemenous and with bicarpellary ovary. A tendency towards production of fertile stamens with unequal length is found in tribe Salpiglossideae. In some of its genera the irregularity of corolla resembles Scrophulariaceae. Passing through Scrophulariaceae the evolutionary tendency leads to a number of closely allied families, viz., Orobanchaceae, Gesneriaceae, Lentibulariaceae and Globulariaceae. Among this evolutionary line the reduction in the number of stamens is a normal feature. The presence of two stamens only in the Lentibulariaceae shows extremely reduced condition. The ovary is bicarpellary or 2-1 locular. Sometimes the reduction in the number of ovules is also discernible, although polyspermous ovary occurs in overwhelming majority.

There is remarkable similarity of embryological features in the order Tubiflorae as a whole. The anther tapetum is glandular. The pollen grains may be 2 or 3-nucleate at the shedding stage. The ovules are usually anatropous, unitegminal and tenuinucellar. There is usually a single hypodermal cell which directly behaves as the megaspore mother cell. The embryo sac generally conforms to the Polygonum type. By virtue of its variability the endosperm has been considered to be of considerable phylogenetic significance. In the supposedly primitive families (Polemoniaceae and Convolvulaceae including Cuscuta) the endosperm is Nuclear. In Solanaceae,

Hydrophyllaceae and Boraginaceae the endosperm is variable. In these families the endosperm may be Nuclear or Cellular and a type intermediate between them. The condition in Loraginaceae is most remarkable, where all the three principal types of endosperm — Nuclear, Cellular and Helobial occur. In highly evolved families the endosperm is generally Cellular. The Cellular endosperm is divisible into two types depending upon the sequence of early cell division and the differentiation of haustoria showing distinct evolutionary sequence. This is well demonstrated in the family Scrophulariaceae (Glisic, 1936-1937; Krishna Ayengar, 1940a, 1940b; Crete, 1951; Banerji, 1961). The embryogeny in the Tubiflorae usually conforms to the Onagrad type but other types also may occur frequently.

The interesting variations of the investigated species of Solanum and the light which these throw on the evolutionary tendencies in its species have been discussed below.

The floral organogeny takes place in acropetal succession in the investigated species of Solanum.

Davis while instituting the four categories of anther wall development in her book entitled "Systematic Embryology of the Angiosperms" mentions usually Dicotyledonous and rarely basic type of anther wall development in Solanaceae. The development of anther wall layers in the present investigation also conforms

to the Dicotyledonous type. Dicotyledonous type of anther wall development has also been reported earlier in Solanum nigrum (Saxena and Singh, 1969a), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. triquetrum (Ahmad and Siddiqui, 1981) and S. Phasianum (Khan and Siddiqui, 1981). Monocotyledonous type of anther wall development has been reported in Nicotiana (Jos and Singh, 1968). In Withania somnifera (See Davis, 1966) and Nicandra physaloides (Prasad and Singh, 1978) the anther wall development follows Basic type. However on the basis of diagrams of Mohan Ram and Kamini (1964) the development of anther wall layers in Withania somnifera appears to follow Dicotyledonous type.

According to Davis (1966) Dicotyledonous and Monocotyledonous types of anther wall development have been derived from Basic type by suppression of the periclinal division in the inner or outer secondary parietal layers. Thus the species described here occupy an advance position in the family.

The epidermis is thin-walled and persistent. It is cutinized in S. douglasii and S. hispidum as reported in Lycium europaeum (Jain, 1956).

The endothecium is generally single layered in S. furcatum and S. douglasii as reported in Lycium europaeum (Jain, 1956) and S. nigrum (Saxena and Singh, 1969a). Multilayered endothecium as described in S. hispidum, S. retroflexum and S. cornutum has also been reported in

Nicotiana tabacum and N. glutinosa (Jos and Singh,1968), S. triquetrum (Ahmad and Siddiqui, 1981)and S. khasianum (Khan and Siddiqui, 1981). The endothecium develops fibrous thickenings except in genera with porous dehiscence (See Davis, 1966). Eames (1961) while commenting on the fibrous endothecium has remarked "Forms transitional to longitudinal dehiscence have some fibrous tissue, restricted usually to areas around the pore-Solanaceae".However fibrous thickenings usually develop at the tip region in S. furcatum, S. retroflexum and S.douglasii as reported earlier in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b). In S. hispidum and S. cornutum the endothecium is completely devoid of fibrous thickenings as reported earlier in S. tuberosum (Young, 1923),Lycium europaeum (Jain, 1956), S. macranthum (Mohan, 1970), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan and Siddiqui, 1981), while in Withania somnifera (Ram and Kamini, 1964) fibrous thickenings develop in the endothecium.

Middle layers are ephemeral and degenerate during the anther maturity as recorded in other members of Solanaceae.

Structurally as well as functionally the tapetum is homogenous in all the described Solanaceae.The glandular tapetum as described in the present materials is a characteristic feature of the family Solanaceae (Smith, 1935; Cochran, 1938; Jain, 1956; Ram and Kamini, 1964;

Jos and Singh, 1968). However, O'Neil (1920) has reported secretory, amoeboid and persistent type of tapetum in Datura stramonium. The tapetal cells are binucleate in the species described here. A similar condition has been reported in S. triquetrum (Ahmad and Siddiqui,1981) and S. khasianum (Khan and Siddiqui, 1981).Multinucleate tapetum as observed in S. furcatum and S. cornutum has been reported in S. nigrum (Saxena and Singh, 1969a).

Namikawa (1919) for the first time observed a resorption tissue in anthers of Solanaceae but most of the subsequent workers (Young, 1923; Smith, 1935; Cochran, 1938; Barnard, 1949; Jain, 1956; Avery et al.,1959; Ram and Kamini, 1964; Jos and Singh, 1968) failed to record it. It has now been described in a large number of lants of the family (Singh and Saxena, 1968; Saxena and Singh, 1969a, b). The author has also observed resorption tissue in S. hispidum and S. cornutum. Resorption tissue is hypodermal in origin. In Solanaceae, the epidermis does not contribute to the resorption tissue Sensu stricto as described in Ericaceae (Matthews and Knox, 1926; Ganapathy and Palser, 1964) and Leguminosae (Venkatesh,1956a, 1956b, 1957).

The number, nature and organization of cells forming the resorption tissue vary in different species. The manner of lysis and the formation of the resorption cavity and the resorption passage between the pollen sacs of an anther lobe clearly demonstrate the primary function of this tissue. It is to bring about the confluence bet-

ween the microsporangia of an anther lobe and to facilitate anther dehiscence (See Singh and Saxena,1968;Saxena and Singh, 1969a,b). The longitudinal dehiscence of anther in Solanaceae is the result of disjunction of cells forming the stomium and not their disintegration.

Artopoeus (1903) has suggested that the lysis of resorption tissue is due to enzyme action, but Namikawa (1919) and Matthews and Knox (1926) attribute it to the action of oxalic acid. The latter author correlate the presence of calcium oxalate crystals in the cells of the connective with the granular material occurring in the cells of the resorption tissue which they regard of the same nature.

The dehiscence of anther in S. furcatum, S. retroflexum and S. douglasii is by apical pore whereas in S. hispidum and S. cornutum it is by apical pore as well as pores formed on longitudinal suture. The presence of resorption tissue in S. hispidum and S. cornutum shows that the resorption tissue develops in species with longitudinal dehiscence of the anther. The porous as well as longitudinal dehiscence of anther in S. hispidum and S. cornutum is the first record and has not been reported earlier in the family.

According to Eames (1965) "poricidal dehiscence has apparently been derived independently in different taxa from longitudinal dehiscence by shortening the slit".Thus S. furcatum, S. retroflexum and S. douglasii are advance where the dehiscence is strictly by means of apical pore

as recorded in majority of the investigated Solanaceae. On the other hand in S. hispidum and S. cornutum in addition to the porous dehiscence, small pores are also formed on longitudinal suture and thus may be considered intermediate.

The hypodermal male archesporium is uniseriate in S. hispidum, S. furcatum, S. retroflexum, S. dougle-sii and S. cornutum. A similar condition has been reported in Lycopersicum (Smith, 1935), Capsicum (Cochran,1938), Lycium (Jain, 1956), Datura (Avery et al., 1959); Withania somnifera (Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968) and S. nigrum (Saxena and Singh,1969a). On the other hand Young (1923) has recorded a 2-layered horse shoe-shaped archesporium in Solanum tuberosum. A careful examination of Young's figure-2, a photomicrograph, which he cited in support of his observation shows transection of a well developed anther with differentiated wall layers and a 2-layered horse-shoe shaped sporogenous tissue. The latter was mistaken by him for the male archesporium.

The number of sporogenous layers in transection is fairly constant and a great similarity exists in microsporogenesis and development of male gametophyte in the described Solanaceae. The microspore tetrads are generally tetrahedral in described Solanums. The occurrence of isobilateral, decussate and rhomboidal microspore tetrads as recorded here in the present investigation has been reported earlier in S. triquetrum (Ahmad and

Siddiqui, 1981) and S. khasianum (Khan and Siddiqui,1981) while isobilateral and decussate types of microspore tetrads only have been recorded in Withania somnifera (Ram and Kamini, 1964), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. serachoides and S. villosum (Saxena and Singh, 1969b), whereas linear microspore tetrad has been reported by Khan (1951) in S. tuberosum.

Pollen grains are shed at 2-nucleate stage in Solanum hispidum, S. furcatum and S. cornutum as reported earlier in Lycium europaeum (Jain, 1956), Withania somnifera (Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), S. nigrum, S. americanum, S. nodiflorum, S. luteum, S. serachoides and S. villosum (Saxena and Singh, 1969b), Micandra physaloides (Prasad and Singh, 1978) and S. khasianum (Khan and Siddiqui, 1981). The pollen grains are shed at 3-nucleate stage in S. retroflexum and S. douglasii as reported in Nicotiana (Goddubnaja-Arnoldi, 1936), Capsicum frutescens var. japanese variegated (Lengel, 1960) and S. triquetrum (Ahmad and Siddiqui, 1981), whereas in Solanum phureja (Unyansagar and Cooper, 1960) the pollen grains are shed at 2- or 3-celled stage. Barnard (1949) reports the degeneration of vegetative nucleus before shedding in Duboisia leichhardtii and D. myoporoides. The pollen grains are thus shed at secondary 1-celled stage. Palynologically the pollen grains are tricolporate in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum as have already been reported in Lycium europaeum (Jain, 1956), Withania somnifera (Ram and Kamini, 1964), Solanum

nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan and Siddiqui, 1981). Occasional occurrence of tetra and multicolporate pollen grains in S. furcatum, S. retroflexum and S. cornutum has been recorded in the family Solanaceae (See Varghese, 1967). Polysiphonous condition and in situ germination of pollen grains as observed in S. cornutum is the first record in the genus Solanum, but have been reported in Lycium europaeum (Jain, 1956) and Withania somnifera (Ram and Kamini, 1964).

The ovary is bicarpellary, syncarpous and bilocular with a massive axile placentation in Solanaceae. In Nicandra physaloides (Prasad and Singh, 1978) the ovary is 5-chambered and the placenta is branched and slender. The ovary contains numerous ovules in Solanaceae but in Lycium europaeum there are 6-8 ovules. Jain (1962) regards that the ovary in Lycium approaches the Convolvulaceae in this feature.

The ovules in Solanaceae are interpreted various-ly. Anatropous ovules as described in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum have been recorded earlier in Nicotiana rustica, N. tabacum and Datura stramonium (Chatin, 1874), Lycopersicon esculentum (Cooper, 1931; Smith, 1935), Solanum melongena (Bhaduri, 1932), Nicotiana plumbaginifolia, Petunia nyctaginiflora (Bhaduri, 1935), Capsicum frutescens var. grossus (Cochran, 1938), Lycium europaeum (Jain, 1956), Capsicum frutescens

var. japanese variegated ornamental (Lengel, 1960), Browallia demissa (Mohan, 1966), Nicotiana tabacum, N. rustica, N. glutinosa, N. glauca, N. megalosiphon, N. trigonophylla, N. longiflora and N. alata (Jos and Singh, 1968) and S. khasianum (Khan and Siddiqui, 1981), whereas it is half anatropous in Brunfelsia americana, Datura fastuosa, Lycopersicum esculentum, Physalis minima, P. peruviana, Salpiglossis sinuata, S. nigrum and Withania somnifera (Bhaduri, 1935). Anacampylotropous ovules have been recorded in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970), Nicandra physaloides (Prasad and Singh, 1978). Both anatropous and campylotropous ovules have been reported in Datura (Avery et al., 1959) and S. phureja (Onyansagar and Cooper, 1960). Campylotropous and amphitropous ovules have been described in Cestrum diurnum and C. nocturnum (Bhaduri, 1935) and S. tuberosum (Rees-Leonard, 1935) respectively.

The female archesporium is usually single celled in Solanaceae (Bhaduri, 1935; Cooper, 1931; Smith, 1935; Cochran, 1938; Jain, 1956; Lengel, 1960; Ram and Kamini, 1964; Jos and Singh, 1968; Prasad and Singh, 1978; Ahmad and Siddiqui, 1981 and Khan and Siddiqui, 1981). Occasional occurrence of 2-celled female archesporium in S. hispidum, S. furcatum, S. retroflexum and S. cornutum has been recorded earlier in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970),

Nicandra physaloides (Prasad and Singh, 1978). Rare occurrence of multicellular archesporium in S. douglasii has been described in S. melongena (Bhaduri,1932), Lycopersicum esculentum, Physalis peruviana,Nicotiana plumbaginifolia, Salpiglossis sinuata and Brunfelsia americana (Bhaduri, 1935), S. tuberosum (Rees Leonard, 1935), Datura (Glisic, 1928; Avery et al., 1959), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan and Siddiqui, 1981). Occurrence of accessory archesporial cells as described in S. hispidum is the first record in the genus Solanum. However, Varghese (1967) has recorded the presence of accessory cells in Solanaceae.

Reduction in the number of archesporial cells is considered an advance character. Thus, Solanum hispidum appears to be primitive in having 1-5-celled archesporium than S. furcatum, S. retroflexum, S. douglasii and S. cornutum, where the archesporium is 1-2-celled.

The development of female gametophyte is of monosporic, 8-nucleate and Polygonum type in the present materials as recorded earlier in Cestrum splendens,Nicotiana tabacum (Guignard, 1882), Atropa belladona (Soueges,1907), Nicotiana (Palm, 1922), Delitebac and Hyoscyamus niger (Svensson, 1926), Lycopersicum esculentum (Cooper, 1931), Capsicum annuum (Banerji, 1931), S. melongena (Bhaduri, 1932), Nicotiana rustica (Mersidsky and Modilewski,1935), Duboisia liechhardtii, D. myoporoides (Barnard, 1949), Lycium europaeum (Jain, 1956), Withania somnifera (Ram and Kamini, 1964; Ariz et al., 1972), Nicotiana tabacum,

N. rustica, N. plumbaginifolia, N. longiflora, N. alata (Jos and Singh, 1968), S. nigrum (Saxena and Singh, 1969a), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan and Siddiqui, 1981). On the contrary Nanetti (1912) in S. muricatum and Young (1923) in S. tuberosum described tetrasporic Adoxa type of embryo sac development. Bhaduri (1932) criticized the observation of Nanetti (1912) and Young (1923) and recorded Polygonum type of female gametophyte development in S. melongena and S. nigrum. On the other hand Modilewski (1935) described 'Scilla' type of embryo sac in Nicotiana glauca but Jos and Singh (1968) have shown that the development follows Polygonum type not only in N. glauca but in other seven species of the genus.

Monosporic type of female gametophyte development as described in the present investigation is considered to be most primitive from which Bisporic and Tetrasporic types have been evolved. However, the development of female gametophyte is Monosporic with a tendency towards Bisporic in Lycopersicum esculentum (Cooper, 1931), Nicotiana glauca (Modilewski, 1935), Withania somnifera (Ram and Kamini, 1964), Cestrum elegans, Capsicum frutescens, Nicotiana rustica (See Davis, 1966) and Tetrasporic in S. muricatum (Nanetti, 1912) and S. tuberosum (Young, 1923). Thus the above mentioned species may be considered under the process of evolution.

Pollination is anemophilous and the entry of pollen tube into the ovule is porogamous in Solanaceae (Dnyansagar and Cooper, 1960; Saxena and Singh, 1969a,b; Mohan, 1970; Prasad and Singh, 1978; Khan et al., 1981) as described in the present investigation. One male gamete fuses with the egg nucleus and second one is seen in the vicinity of secondary nucleus in S. furcatum, S. retroflexum and S. douglasii while in S. hispidum and S. cornutum the second male gamete fuses with the polar nuclei. Fusion of polar nuclei before fertilization has also been reported in Petunia (Cooper, 1961), S. phureja (Dnyansagar and Cooper, 1960), S. triquetrum (Ahmad and Siddiqui, 1981) and S. khasianum (Khan et al., 1981).

On the contrary Ferguson (1927) described that in Petunia nyctaginiflora secondary nucleus divides before fertilization and that the second male gamete fuses with the nucleus of micropylar cell. According to her (1927) one fourth of the growing endosperm derived from the micropylar cell is triploid and the remainder is diploid. However, Cooper (1946) re-investigated two varieties of Petunia, Elk's Pride and Topaz Queen and reported that double fertilization takes place in usual manner and the entire endosperm is triploid.

The development of endosperm in Solanaceae conforms to Cellular, Nuclear and Helobial (See Davis, 1966). The development of endosperm in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum is ab initio Cellular as recorded earlier in Atropa, Datura, Salpiglossis variabilis and Scopolia (Dahlgren, 1923), Petunia (Cooper, 1946),

S. phureja (Dnyansagar and Cooper, 1960), Lycium europaeum (Jain, 1962), Withania somnifera (Ram and Kamini, 1964), Nicotiana (Jos and Singh, 1968), S. nigrum (Saxena and Singh, 1969a), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b), S. macranthum (Mohan, 1970), Nicandra physaloides (Prasad and Singh, 1978) and S. khasianum (Khan et al, 1981). On the contrary Nuclear type of endosperm development has been recorded in Hyoscyamus orientalis, Salpiglossis and Scopolia atropoides (Hofmeister, 1958), Schizanthus pinnatus (Samuelsson, 1913; Dahlgren, 1923), Lycium barbarum (Persidsky, 1935), Capsicum frutescens var. grossus (Cochran, 1938) and S. triquetrum (Ahmad and Siddiqui, 1981). Svensson (1926) described Cellular as well as Helobial types of endosperm development in Hyoscyamus niger in which the micropyler chamber is small and the chalazal is large. The early divisions in the chalazal chamber are always free nuclear forming 26-30 nuclei and in micropylar chamber variations in the type of divisions have been observed. The divisions may be free nuclear or each division followed by wall formation or the first division is by a vertical wall followed by free nuclear divisions. The second condition is more frequent than the first and third types. In Hyoscyamus niger (Svensson, 1926) most of the endosperm is produced by large chalazal chamber. Barnard (1949) also feels that probably the endosperm development is Helobial in Duboisia leichhardtii and D. myoporoides. According to him (1949) "After fertilization the endosperm nucleus

migrates to the chalazal end and divides a number of times before the division in zygote.Several densely cytoplasmic endosperm cells settle at the bottom of the sac and form a base upon which a free nuclear endosperm develops".

The first division in primary endosperm cell is transverse in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum as recorded earlier in Datura laevis (Guignard, 1902), Petunia nyctaginiflora (Cooper, 1946), Withania somnifera (Ram and Kamini, 1964), Nicotiana tabacum (Jos and Singh, 1968), S. macranthum (Mohan, 1970), Nicandra physaloides (Prasad and Singh, 1978) and S. khasianum (Khan et al., 1981), while in Petunia nyctaginiflora, Lycopersicum esculentum (Bhaduri, 1933), S. macranthum (Mohan, 1970), S. phureja (Dnyansagar and Cooper, 1960) the first division in primary endosperm cell is longitudinal. The second division in primary endosperm chambers is longitudinal in the present materials,whereas in S. macranthum (Mohan, 1970) and Nicandra physaloi- des (Prasad and Singh, 1978) the division in both the primary endosperm chambers is transverse.

Occasional T-shaped arrangement of four cells of the endosperm as described here in S. furcatum, S.retroflexum S. douglasii and S. cornutum has been recorded earlier in S. khasianum (Khan et al., 1981). Rare occurrence of linear arrangement of four cells of endosperm as observed in S. furcatum and S. douglasii has been described as a normal feature in S. macranthum (Mohan, 1970)and Nicandra

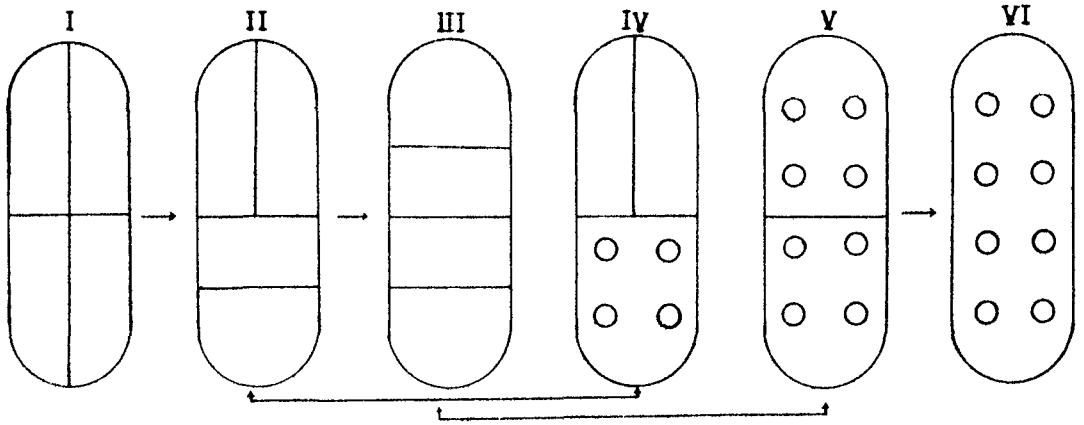
physaloides (Prasad and Singh, 1978). The inverted T-shaped arrangement of four cells as observed in S. retroflexum and S. cornutum has not been reported elsewhere in the family.

The plane and sequence of cell divisions from 4 to 8 celled endosperm as recorded in S. furcatum, S. retroflexum and S. douglasii has only been reported in S. phureja (Dnyansagar and Coopor, 1960) where the first two divisions are longitudinal forming four tubular cells placed side by side. The third division is transverse forming 8 cells with totally different arrangement.

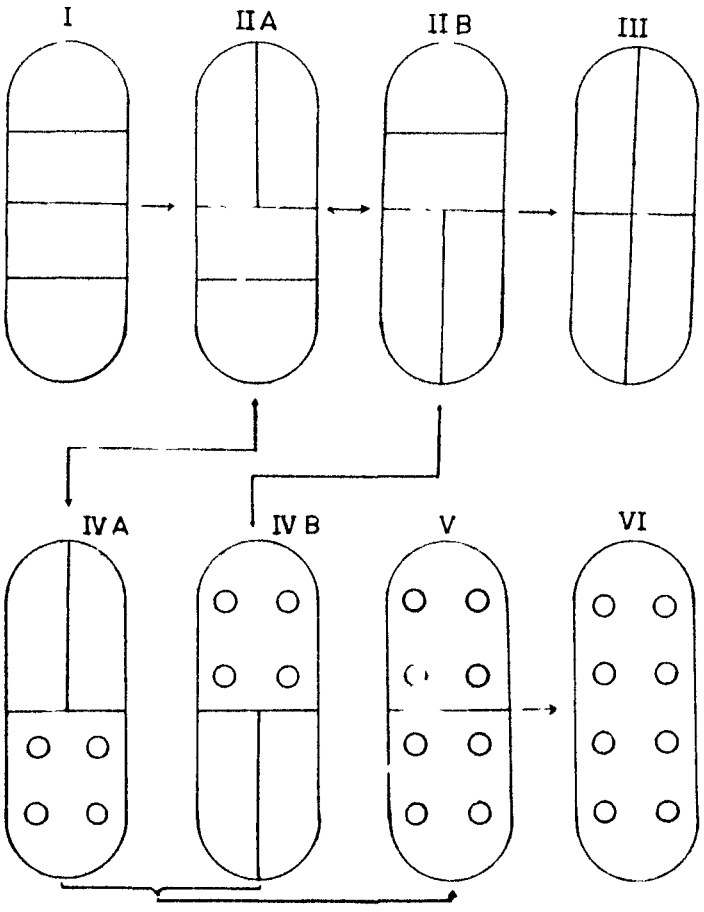
Rosen (1947) while commenting upon the endosperm in Tubiflorae recognizes six types of endosperm in Solanaceae. His types I-VI are presented in figure which also give their relationships. Rosen (1947) regards Cellular endosperm to be the most primitive type and the Helobial and Nuclear derived from it. Cellular is the common type of endosperm in the family, whereas the other two types are rare and in some cases need confirmation. Among the Cellular types, Rosen (1947) believes that his type I is the most primitive and compares it with the 'Verbascum' type of Scrophulariaceae. Type I is characterized by vertical divisions in both the chambers of 2-celled endosperm. However, the occurrence of transverse divisions in 2-celled endosperm in Nicandra physaloides which fits in well under the type III of Rosen (1947) deserves careful consideration in any assesment of phylogenetic relationships of endosperm in this family. Nicandra belonging

to the tribe Ricandrae, occupies a primitive position in modern classification of the family (Wettstein, 1935). It also shows many primitive features in its morphology and life history namely, trifurcate stamen supply, 5-carpellary and 5-locular ovary, thin placenta, persistent pollen tube, thin walled persistent endothelium and a number of hypodermal layers persisting in seed coat. These facts and a recent critical discussion on endosperm in Veronica by Tiagi (1966), who regards the endosperm development in Veronica longifolia in which transverse division takes place in the micropylar chamber at the second cell generation, as primitive, has led the present author to believe that type III, of Rosen (1947) represents the most primitive condition of endosperm in Solanaceae. It may be pointed out that Rosen's Type IV and V are only known as abnormalities in Hyoscyamus niger (Svensson, 1926). They have not been considered by any other worker so far.

Considering Rosen's (1947) assumption that Nuclear type of endosperm has been derived from Cellular type, the author has also presented a scheme, which differs from Rosen (1947) scheme. In the present scheme the type III, which is type I of Rosen, is considered as most advanced Cellular type. Considering the scheme presented by the author Solanum hispidum occupies an advance position where the endosperm development strictly conforms to type III. In S. furcatum and S. douglasii in addition to type III, type I and type IIA have also been observed



ROSEN (1947)



AUTHOR'S VIEW

DIAGRAMMATIC REPRESENTATION OF THE PROBABLE EVOLUTIONARY SEQUENCE OF THE ENDOSPERM TYPES IN SOLANACEAE

and thus have been considered to be most primitive amongst the species studied by the author. In S. retroflexum and S. cornutum besides type III type IIA and IIB have also been observed and occupy intermediate position. The types IVA and IVB are considered to be derived from IIA and IIB respectively from which type V and VI have been derived.

Nicotiana variation of Solanad type of embryogeny as described in S. furcatum, and S. douglasii has been recorded earlier in S. tuberosum, Datura stramonium, Physalis edulis and Atropa belladona (Tognini, 1900), Nicotiana, Hyoscyamus, Datura and Atropa (Soueges, 1920a,b,1922)Nicotiana rustica (Persidsky and Modilewski,1935; Modilewski, 1937), Physalis minima, Withania somnifera and Petunia nyctaginiflora (Bhaduri, 1936), Schizanthus and Petunia (Soueges, 1936), Physalis peruviana (Crete, 1954), Solanum demissum (Walker, 1955), Saracha jaltomato (Crete, 1960), S. phureja (Dnyansagar and Cooper, 1960), Datura tetula (Crete, 1961a), Browallia demissa (Crete, 1961b),Salpiglossis sinuata (Crete, 1961d), S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S.villosum(Saxena and Singh, 1969b), S. triquetrum (Ahmad and Siddiqui,1981), S. khasianum (Khan et al., 1981). Myosotis variation of Chenopodiad type of embryogeny as described in S.hispidum, S. retroflexum and S. cornutum has not been recorded earlier in the family Solanaceae. Rare occurrence of Ruta variation of Onagrad type in S. furcatum and S.retroflexum has been recorded as a usual feature in Capsicum annuum (Crete, 1961c).

The occurrence of adventive embryos from the cells of endothelium as observed in S. hispidum has been recorded earlier in S. macranthum (Mohan, 1970). Adventive polyembryony has also been recorded earlier in Petunia nyctaginiflora, Withania somnifera and Nicotiana plumbaginifolia (Banerji and Bhaduri, 1933) and N. tabacum (Jos and Singh, 1968). Both these authors considered the additional embryos to be of nucellar origin. Recent studies of the development of ovule and seed in Solanaceae by Saxena and Singh (1969a,b), Prasad and Singh (1978), Ahmad and Siddiqui (1981) and Khan et al (1981) and the present study clearly show that the nucellus is completely absorbed at 2-nucleate embryo sac stage. Thus there is no trace of nucellus in fertilized ovules and accordingly nucellar origin for accessory embryos appears to be incorrect . Cooper (1943) on the basis of haploid seedlings in interspecific hybridization in Nicotiana regards the accessary embryos of synergid origin. Cameron (1949) also observed polyembryony in Nicotiana tabacum seedlings having different chromosome number.

Production of embryos from antipodal cells is much rare. Occurrence of antipodal embryos in S. cornutum has not been recorded in Solanaceae. Shattuck (1905) noted in Ulmaceae that the antipodal cells of Ulmus americana often present an egg like appearance and in some cases he actually found embryos in this position.

The development and structure of seed in the present materials broadly resemble the other investigated Sola-

naceae (Soueges, 1907; Netolitzky, 1926; Dnyansagar and Cooper, 1960; Saxena and Singh, 1969a,b; Mohan, 1970; Prasad and Singh, 1978; Khan et al., 1981), but differ in minor details. Soueges (1907) described the development and structure of seed coat in 146 species belonging to 26 genera of Solanaceae including those of Atropa, Datura, Hyoscyamus, Nicotiana, Scopolia and Solanum. During seed development the cells of the middle layers of integument degenerate completely in S. hispidum, S. furcatum, S. douglasii and S. cornutum, while in S. retroflexum 5-8 middle layers persist in the mature seeds. The persistent middle layers have been recorded in the seed coat in Cursicum (Soueges, 1907) and Cochran (1938), S.nigrum(Saxena and Singh, 1969a), Nicandra physaloides (Prasad and Singh, 1978) and S. khasianum (Khan et al., 1981). Similarly in S. phureja (Dnyansagar and Cooper, 1960) the cells of the integument degenerate and only the compressed cell walls persist out side the endothelium. Complete degeneration of integument layers in the seed coat has also been recorded in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S. villosum (Saxena and Singh, 1969b).

The single layered endothelium degenerates during seed development in S. furcatum, S. retroflexum and S. cornutum, while it persists in S. douglasii and develops fibrous thickenings. In S. hispidum the endothelium becomes 3-4 layered and their walls become highly lignified. Single layered persistent endothelium with fibrous thick-

enings has been reported earlier in S. nigrum, S. americanum, S. luteum, S. nodiflorum, S. sarachoides and S.villosum (Saxena and Singh, 1969b). whereas single layered thin walled persistent non-fibrous endothelium has been reported in S. nigrum (Saxena and Singh, 1969c) and Nicandra physaloides (Prasad and Singh, 1978). On the other hand endothelium degenerates during seed development in Nicotiana, Nicandra and Lycium (Bouegeo, 1907), S. macranthum (Mohan, 1970) and S. khasianum (Khan et al., 1981).Occurrence of 3-4 layered thick walled endothelium in S.hispidum has not been recorded earlier in the family.

The epidermis in the mature seed is single layered in the described Solanaceae (Lanyensegar and Cooper, 1960; Saxena and Singh, 1969c,b; Mohan, 1970; Prasad and Singh, 1978; Khan et al., 1981) as observed in S. hispidum, S. furcatum and S. cornutum, while at places it becomes 2-layered in S. retroflexum and 2-3-layered in S. aculeatissii. Multiplicative epidermis is the first record in the family Solanaceae. The seeds are endospermic in the present materials. In S. retroflexum the endosperm extends between the coiled embryo and is characterized by a bulbous comma head and a slender comma stem as recorded earlier in Nicandra physaloides (Prasad and Singh, 1978).

As summarised earlier, divergent views have been put forward on the systematic position of the Solanaceae(Engler and Prantl, 1895; Bentham and Hooker, 1873-76;Bessey,1893; Wettstein, 1935; Gundersen, 1950; Wendle, 1952; Benson, 1957; Porter, 1959; Hutchinson, 1959, 1964; Melchior,1964; Takhtajan, 1966; Cronquist, 1968). Majority of the workers

recognize close resemblences of Solenaceae with Nolanaceae, Convolvulaceae and Scrophulariaceae. The salient embryological features of Solanaceae are thus compared with those of the above families.

Convolvulaceae differs from Solanaceae in having Nuclear endosperm, embryo with massive suspensor and folded cotyledons, seed coat differentiates into four zones and the sub-epidermal origin of the main mechanical layer. Palynologically also Convolvulaceae are different from Solanaceae (Erdtman, 1952). Hence any close affinity between Solanaceae and Convolvulaceae seems to be out of question.

Scrophulariaceae and Nolanaceae show strong affinities with Solanaceae in embryological features. A perusal of literature shows that Scrophulariaceae differs from Solanaceae in Cellular endosperm with well developed micropylar as well as chalazal haustoria and Onagrad type of embryogeny (Banerji, 1961; Tiagi, 1966). As the features of corolla it compares with tribe Salpiglossideae (Solanaceae) which is regarded to form a link between the two families (Wendle, 1952; Takhtajan, 1966). Absence of micropylar and chalazal haustoria in Mimulus cardinalis and Scrophularia marylandica and Soland type of embryogeny in Ellisiophyllum innatum (see Davis, 1966) are known in Scrophulariaceae. Similarly rudimentary endosperm haustoria have been doubted in Solanum dhureja (Dnyansager and Cooper, 1960). In addition the pollen grains similar to those of Solanaceae occur in Scrophulariaceae (Erdtman, 1952). Though it may be pointed out that embryologically Salpiglossideae is still inadequately

investigated, nevertheless, the available data show great plasticity in morphological and embryological features of the tribe which may well be treated a potential progenitor of Scrophulariaceae.

The Nolanaceae share maximum common features with Solanaceae. However, Solanaceae differ from Nolanaceae mainly in the structure of the ovary and fruit. The schizocarpic, horny and nutlet-like fruit of Nolanaceae is unlike any Solanaceae but approaches the Boraginaceae. The endosperm development in Nolana is ab initio Cellular but at the second cell generation the division is by vertical walls (Rosen, 1947). The present investigator recognizing the close resemblances and anomolous features of Nolanaceae, favours its origin from Solanaceous stock parallel to Boraginaceae.

Wettstein sub-divided Solanaceae into five tribes; Nicandreae, Solaneae, Datureae, Cestreae and Salpiglossideae. Bentham and Hooker (1873-76) have also grouped the genera of Solanaceae under five suborders (tribes)- Solaneae, Atropeae, Hyoscymeae, Cestrineae and Salpiglossidece. The former classification is mostly followed by the modern taxonomists (Rendle, 1952; Hutchinson, 1959; Takhtajan, 1966; Willis, 1966). Basak (1967) on the basis of pollen morphology of 93 species belonging to 28 genera of Solanaceae, has shown that there are striking differences between the pollen grains of Nicandreae, Solaneae, Datureae, Cestreae and Salpiglossideae. Embryologically Nicandreae, Solaneae and Datureae form a homogenous group

which differ from Cestreae and Salpiglossideae in having anacampylotropous ovules, Cellular endosperm, coiled embryo and persistent endothelium. Cestreae and Salpiglossideae, on the other hand, are characterized by anatropous ovules, Cellular, Helobial or Nuclear endosperm, straight or only slightly bent embryo and ephemeral endothelium. Bouegeo (1907) described ephemeral endothelium in the genera of Cestreae except Cestrum and Salpiglossideae. The flower in the former group is always actinomorphic having five fertile stamens whereas in the latter it shows a tendency to zygomorphy and reduction in the number of stamens. Obviously, therefore, embryology seems to point to a polyphyletic origin of Solanaceae as interpreted by Wettstein (1935).

Nicandreae having 3-5 locular ovary, trifurcate staminal supply, Basic type of anther wall development, absence of differentiation of resorption tissue, multi-celled female archesporium, Cellular endosperm with transverse divisions at the second cell generation, multi-layered seed coat and thin walled endothelium represent the most primitive tribe of the family. Nicandreae having the monotypic genus Nicandra also stand apart from all other tribes in the structure of pollen grains (Basak, 1967).

Salpiglossideae including genera with strongly zygomorphic bilipped corolla, reduction in the number of fertile stamen, Nuclear, Helobial and Cellular endosperm and ruminate or non-ruminate coat, form an advance tribe in the family.

The comparative embryological features of the Solanum species investigated here have been given in the tabular form which could be helpful in the identification of the species. Evolutionary trends in the genus Solanum itself have also been brought out. Considering the number of species included in the genus Solanum and the paucity of the embryological data it is rather difficult to reach any definite conclusion. However, it appears that intensive comparative morphological studies in this interesting group of plants would show a complete sequence of evolution within the genus and the relationships of the latter with other genera of the family.

SUMMARY

The embryology of *Solanum hispidum* Pers., *S. furcatum* Dun., *S. retroflexum* Dun., *S. douglasii* Dun. and *S. cornutum* Lam. has been described.

1. The habit, external morphology and inflorescence of the above mentioned species have been described.

2. The flowers are pentamerous and actinomorphic in *S. hispidum*, *S. furcatum*, *S. retroflexum* and *S. douglasii* while in *S. cornutum* the flowers are zygomorphic. Occasionally the flowers may be tetramerous in *S. hispidum*. The calyx lobes are gamosepalous, bell-shaped and persistent in all the species described here. The calyx is accrescent in *S. cornutum*. The corolla is gamopetalous and campanulate in *S. hispidum*, *S. furcatum*, *S. retroflexum* and *S. douglasii*. However in *S. cornutum* the corolla is zygomorphic. The stamens are epipetalous. The anthers are bithecous and 4-chambered. The ovary is bicarpellary, syncarpous and bilocular with swollen axile placenta. The stigma is capitate in *S. furcatum*, *S. retroflexum* and *S. douglasii* while in *S. hispidum* and *S. cornutum* it is lobed. Heterostyly has been observed in *S. hispidum*. The fruit is berry.

3. The floral organogeny takes place in acropetal succession.

4. The anthers are quadrangular in transection. The development of anther wall layers in all the five species conforms to the Dicotyledonous type. In a mature anther

three layers of cells intervene the epidermis and sporogenous layer. The endothecium is single layered in S. furcatum and S. douglasii, 2-layered in S. retroflexum, 4-layered in S. hispidum and 2-4-layered in S. cornutum. The endothecium is devoid of fibrous thickenings except in the tip region. Next to the endothecium is middle layer which is single layered in S. retroflexum, 2-layered in S. hispidum and S. furcatum, 3-layered in S.douglasii and 2-4-layered in S. cornutum. These layers are sandwitched between the endothecium and the tapetum.The tapetum is generally binucleate in all the species,sometimes 2-4 nucleate in S. furcatum and S. cornutum. The tapetum and middle layers degenerate during the development of pollen grains.

The dehiscence of the anther is porous in S.furcatum, S. retroflexum and S. douglasii and porous as well as by longitudinal slit in S. hispidum. In S. cornutum the dehiscence is porous as well as with the help of pores formed at different intervals in the longitudinal suture. 5. The microspore mother cells undergo meiosis.The divisions in all the microspore mother cells of an anther may not be synchronous. Thus different divisional stages of microsporogenesis have been observed in all the four chambers of the same anther.

The microspore tetrads are tetrahedral, occasionally they may be isobilateral in S. hispidum, S.douglasii and S. cornutum and decussate in S. furcatum and S.retrofle-

xum. Rarely rhomboidal and decussate arrangements have been observed in S. hispidum, S. douglasii and S. cornutum. Isobilateral and rhomboidal microspore tetrads may rarely occur in S. furcatum and S. retroflexum.

Generally the pollen grains are tricolporate in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum. Tetracolporate pollen grains may also occur in S. furcatum, S. retroflexum and S. cornutum. Multicolporate pollen grains have been observed in S. retroflexum.

Variations in the number and size of the nuclei in the pollen grains have also been observed. The p pollen grains are shed at 2-nucleate stage in S. hispidum, S. furcatum and S. cornutum, while in S. retroflexum and S. douglasii they are shed at 3-nucleate stage.

Polysiphonous condition and in situ germination of pollen grains have been observed in S. cornutum. Pollen sterility is more common in S. hispidum.

6. The ovules are anatropous, unitegmic and tenuinucellate. The innermost layer of the integument differentiates as endothelium in all the five species. Hypostase has been observed in the species described here. It persists upto the mature embryo sac stage and degenerates after fertilization.

7. The female archesporium is hypodermal in origin. It is usually 1-celled in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum. Occasionally it may be 2-celled in S. hispidum, S. furcatum, S. retro-

flexum and S. cornutum, 3-celled in S. douglasii and S. cornutum and upto 5-celled in S. hispidum. Accessory archesporial cells have been observed in S.hispidum and S. douglasii. The archesporial cell directly functions as megaspore mother cell. The megaspore mother cells undergo meiosis and produce megaspore tetrads.The megaspore tetrads are generally linear in S. hispidum, S. furcatum, S. retroflexum, S. douglasii and S. cornutum. Sometimes the megaspore tetrads may be T-shaped in S. furcatum. Inverted T-shaped megaspore tetrads may rarely develop in S. hispidum and S. cornutum. In an exceptional case in S. retroflexum an isobilateral megaspore tetrad has been observed. In another case the megaspore tetrad may be almost rhomboidal in S. cornutum. Polyspory has been observed in S. hispidum.

Usually the chalazal megaspore is functioning and the remaining three degenerate. Considerable variations in the number and position of healthy megaspores in a tetrad have been observed in S. hispidum, S.furcatum,S. retroflexum, S. douglasii and S. cornutum.

8. The development of female gametophyte is of monosporic 8-nucleate Polygonum type in the species described here. The polar nuclei fuse before the entry of pollen tube into the embryo sac in S. furcatum, S. retroflexum and S. douglasii while in S. hispidum and S. cornutum they fuse at the time of fertilization. The antipodal cells are ephemeral. Variations in the number of embryo sac nuclei and their organization have also been obser-

ved in S. furcatum, S. retroflexum and S. cornutum. Twin sacs have been observed in S. retroflexum.

9. Pollination is anemophious. The pollen grains germinate on the stigma . The pollen tubes creep between the stigmatic papillae and enter the stylar tissue.They grow down through the intercellular spaces of the stylartissue, reach the ovarian cavity and finally enter the ovules through the micropyle.

One synergid is usually destroyed during the entry of the pollen tube into the embryo sac. Later the other synergid also is destroyed during the act of fertilization. One male gamete fuses with the egg and the other with the secondary nucleus in S. furcatum, S.retroflexum and S. douglasii, while in S. hispidum and S.cornutum the second male gamete fuses with the polar nuclei simultaneously.

10. The development of endosperm is ab initio Cellular in S. hispidum, S. furcatum, S. retroflexum, S.douglasii and S. cornutum. The first division in the primary endosperm cell is transverse forming a primary micropylar and primary chalazal endosperm chambers. The division in both the primary endosperm chambers is longitudinal.The development of endosperm in S. hispidum could not be followed successfully after 4-celled stage because of abnormal behaviour of endothelium, whose cells proliferate and produce adventive embryos.

The second division in the primary micropylar and

primary chalazal endosperm chambers is longitudinal producing 8-celled endosperm in S. furcatum. In S.retroflexum the second division in the primary micropylar endosperm chamber is transverse while in chalazal endosperm chamber the division is longitudinal. In S.douglasii the second division in the cells of primary micropylar and primary chalazal endosperm chambers is transverse. The divisions become irregular after the 4-celled endosperm in S. cornutum.

Considerable variations in the plane and sequence of early cell divisions in the development of endosperm have been observed in S. furcatum, S. retroflexum, S. douglasii and S. cornutum.

11. The proembryonic tetrads are linear and the embryogeny conforms to the Myosotis variation of Chenopodiad type in S. hispidum and S. cornutum. The embryogeny in S. furcatum, S. retroflexum and S. douglasii conforms to the Nicotiana variation of Solanad type. However, Myosotis variation of Chenopodiad type of embryogeny may sometimes occur in S. retroflexum.

The proembryonic tetrads may sometimes be T-shaped in S. furcatum and rarely in S. retroflexum and S. cornutum and the embryogeny conforms to Ruta variation of Onagrad type.

Variations in the number and position of cotyledons in the mature embryos have been observed in S. hispidum. Polyembryony has been observed in S. hispidum. In addi-

tion to the zygotic embryo a number of adventive embryos may arise from the endothelium. In one exceptional case twin sacs developed in the same ovule. In one sac normal zygotic linear proembryonic tetrad developed while in the other the cavity of the embryo sac is completely filled with endothelial embryos.

Rarely the antipodal cells may divide, redivide and form an undifferentiated embryonal mass of cells at the chalazal end of the embryo sac in S. cornutum.

12. The ontogeny and structure of seeds have been described. The mature seeds are kidney-shaped. Anatomically the seed comprises a seed coat, persistent endosperm and a mature curved dicotyledonous embryo.

The seed coat comprises an epidermis in S. furcatum and S. cornutum, while in S. retroflexum the seed coat consists of an epidermis and 5-8 layers of integument. In S. hispidum the seed coat consists of an epidermis and 3-4-layered thick walled endothelium, while in S. douglasii the persistent endothelium is single layered with fibrous thickenings. The endothelium degenerates during seed development in S. furcatum, S. retroflexum and S. cornutum.

The epidermis of seed coat is main mechanical layer. It is single layered in S. hispidum, S. furcatum and S. cornutum and at places it becomes 1-2 layered in S. retroflexum and S. douglasii. The cells of the epidermis develop sclerotic thickenings in the inner portion while

the outer region develops only rod-like fibrous thickenings.

The cells of the persistent endosperm possess starch grains and reserve food material in all the species described here. The endosperm in S. furcatum, S. retroflexum, S. douglasii and S. cornutum occupies a large portion of interior space of the seed and extends between the coiled embryo and this part of endosperm is characterized by a bulbous coma head and a slender coma stem.

13. The affinities of the Solanaceae with the allied families on the basis of embryological features have been discussed. Also the evolutionary trends in the genus Solanum itself have been brought out.

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